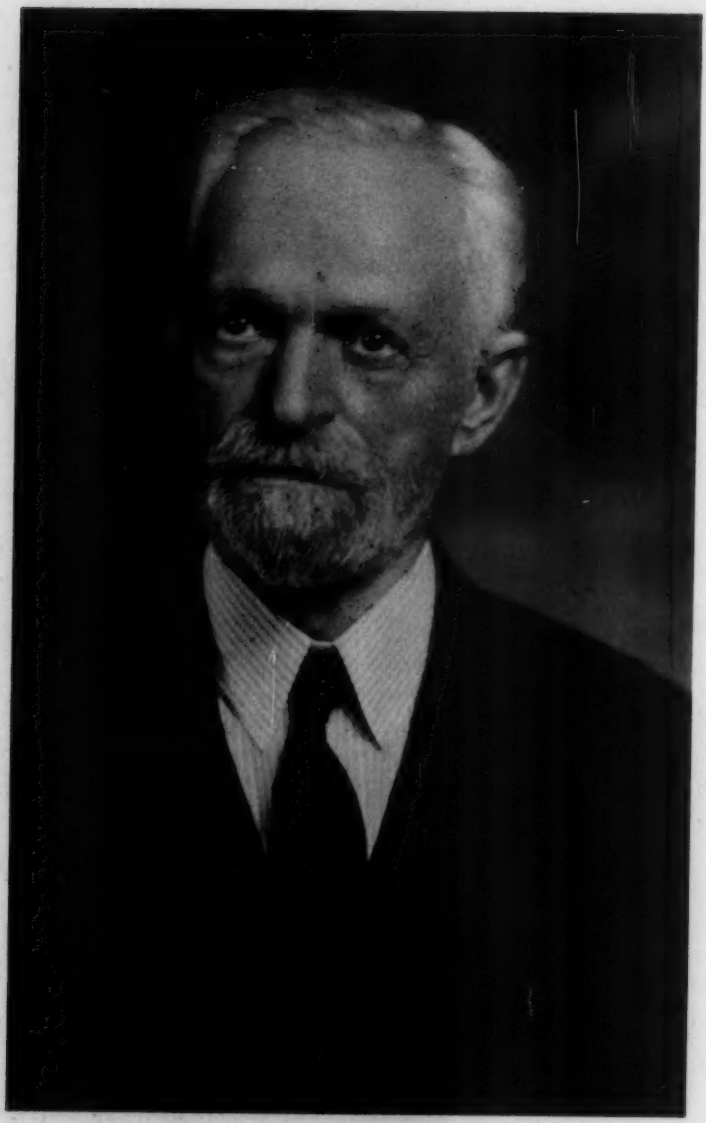

JOHN DEARNESS, PRESIDENT 1937

MYCOLOGIA

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

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THE BACKGROUND OF MYCOLOGY AND OF MYCOLOGIA

BOTH SHOULD BE MORE WIDELY KNOWN

JOHN DEARNESS[1]

(WITH PORTRAIT)

This address is intended to be supplementary to the informative one which President Dr. H. M. Fitzpatrick presented last year, reviewing the historical background of the Mycological Society of America. He showed that the Society had led a kind of discontinuous existence for over thirty years, under three different names, each, however, incorporating the term derived from the name of the Science. So far as I know the only sister society having an earlier history is the Societe Mycologique de France which was organized in 1884.

The Science of Mycology and the Mycological Society of America should both be more widely known than they seem to be. This fact may be accounted for in part by the organization in 1908 and the subsequent continuous activity of the American Phytopathological Society. The latter started with 130 members during a suspension of this Society and has now a membership of over seven times the charter number.

It hardly need be said that in the numerous diseases of economic plants caused by parasitic fungi the pathologists and

[1] Address of the Retiring President of the Mycological Society of America, December 29, 1937, at the Indianapolis meeting of the American Association for the Advancement of Science.

[MYCOLOGIA for January–February (30: 1–110) was issued February 1, 1938]

mycologists are about equally concerned. There is, however, this difference that the former place the emphasis on the effects and cure of the disease while the latter emphasize the life-history and relations of the causative fungus. Each works in a large field outside of the common ground. Pathologists meet with nutritional, climatological and parasitic diseases of plants caused by insects, eelworms and others of animal origin. Numerically the fungus parasites of economic plants form but a small although important section of the extensive field of the mycologists. The organizations of the two classes of workers—the Phytopathological and the Mycological Societies—can and do cooperate to their mutual benefit. This statement will be supported by any one who has the opportunity and uses it to compare even the indexes of their respective official organs. He will find many topics and articles in the 27 volumes of PHYTOPATHOLOGY and in the 29 volumes of MYCOLOGIA [2] that should be highly useful to most of the members of both Societies. Indeed their constituencies might be extended to include students in these branches of science in every country for fortunately the language in which they are published can be read by biologists in nearly every college in the world.

Speaking for Mycology neither the Science nor the Society which bears its name is so generally known or appreciated as it should be. A chance conversation with a well-informed acquaintance and its sequel convinced me that as mycologists we should consider whether we should and can do something to improve our position. Part of the conversation is here recalled:

"I read in the newspaper that you were recently elected to a new office."

"To what office do you refer?", I inquired.

[2] MYCOLOGIA appeared as a bi-monthly in January 1909 published by The New York Botanical Garden under the editorship of Dr. Wm. A. Murrill who in 1924 was succeeded by Dr. F. J. Seaver, the present editor. It became the official organ of the Mycological Society of America in 1933. It is virtually a continuation of the JOURNAL OF MYCOLOGY launched as a venture by Dr. W. A. Kellerman, J. B. Ellis and B. M. Everhart as a monthly in 1885 and continued until Dec. 1888. In 1889 and 1890 it was published as a quarterly by the U. S. Dept. of Agriculture and for the next four years as an annual Bulletin by the same Department. In 1902 its publication was resumed as a bi-monthly by Dr. Kellerman and carried on by him until his death in February 1908

"That is what I was going to ask you. It was at a meeting in Atlantic City."

"Then you mean an office in the Mycological Society of America."

"Yes; I have a dictionary and an encyclopedia in neither of which could I find what kind of society a mycological society is."

His statement surprised me enough to use the next occasion of visiting the reference section of our Public Library to discover what measure of attention the encyclopedists are giving to Mycology and Mycological Societies. Seven of them were consulted.

Chambers'—a general favorite periodically revised: "Mycology" not in alphabetic place in either of two editions examined.

Popular Science—15 Vols.: "Mycology" not in the Index volume.

The Grolier Book of Knowledge—20 Vols.: "Mycology" not in the Index volume.

Encyclopaedia Britannica: Neither "Mycology" nor "Mycological Societies" found in indexes or alphabetic place in the last four editions.

American—16 Vols., 1904: No Article on Mycology.

Nelson's Perpetual: The only mention found was in the article on Anton de Bary—"the founder of the science of Fungi (Mycology)."

Universal Encyclopedia: Mycology in Vol. 9 is dismissed with four lines. In an article on Poisoning by Fungi in another volume there are brief descriptions of each of only four poisonous kinds: *Amanita phalloides* and *muscaria*, *Russula integra* and *Boletus luridus*. Without discrimination of the toxicity of the four the article proceeds to state that symptoms of poisoning will appear in six to eight hours and death may occur in a few hours or may be delayed for two or three days. The well-known condemnation of half truths applies here if McIlvaine can be trusted. He says that *Russula integra* is often astringent but equally excellent with *R. alutacea* and that *Boletus luridus* has a bad reputation but it is edible by some people.

Coming nearer home—Dr. Fitzpatrick in the previously cited address stated that in the first thirty-four years of the

A. A. A. S. only two papers dealing with any phase of mycology were presented. What is the explanation of this neglect or oversight? The fungi, its subject matter, have long been distinguished from other plants and observed. The name is historic, possibly prehistoric. The ancient Romans used it in the same form that we do. Some authorities believe that it is derived from the ancestor of a Greek word meaning the interment of the dead and so making the words "fungus" and "funeral" kin to each other. Even the cavemen may have observed that the fungi are active in returning plants and animals to the dust from which they came.

What the insect has done and can do has been honored by a beautiful monument in a southern city but long before that event a fungus-deity received human worship. The punishment administered to offending husbandmen by the divine Robigus was the blighting of their cereal crops. The Romans imagined that they could court his favor or avert his wrath by the May ceremonials which were known as the Robigalia. Probably de Candolle had these in mind when he named a common barley and wheat rust—*Puccinia rubigo-vera*—the true rubigo. The name suffered partial eclipse in the rust number of the North American Flora but its prestige has been fully restored by one of our editors, Dr. E. B. Mains, who has usefully covered 106 pages to tell the story of its variability and adaptations—a record in the taxonomy of a fungus.

"Moth and rust [3] doth corrupt" is the accepted translation of σης καὶ βρῶσις αφανίζει, Matthew VI: 19. It seems to me that "moth and rust" is here intended for a synecdoche of "insects and fungi," and that a reasonable and defensible exegesis of the Greek words would be insects and fungi make away stealthily with riches in clothing and food. Speaking of fungi as food may recall the story that a fungus of well known properties was a factor in changing for the worse the none too good character of the Imperial Roman government when the detestable Agrippina used it to bring her more detestable son Nero to the throne of the Caesars. It was like him to refer to this fungus after the deification of his ill-fated father as the "food of the gods."

[3] The rust of metals, see James V; 3, is not the Greek word βρῶσις but ἰος a quite different word.

As fungi for human food the self-reported experience of Schwaegrichen may serve for an example. He was an eminent German botanist who lived about a century and a half ago. He wrote to a friend that he had imitated the Nurembergians in their eating of raw fungi and that for several weeks he ate nothing but their black bread and raw fungi and drank nothing but water with the result that he quite recovered his health and strength.

It could not have been otherwise than that fungi and their effects have always been objects of observation, suspicion and even affection. Linnaeus the great classifier observed them and related some of them to their congeners in giving them binomial names; Persoon went much further in the same direction. But these naturalists were only in the twilight of the science of Mycology. Donald C. Peattie, a good, present-day phanerogamist possibly at this meeting, in his very readable book, "Green Laurels," speaking of the curious reactions of the old herbalists to the then unclassified green plants, has this to say—"Perhaps the best way to feel plants as those old fellows felt them is to go mushrooming—for the fungi have about them something evanescent, deathy, alluring, two-faced, and still largely unknown." Marshall Ward, the foremost British mycologist, referring to an event that took place within the lifetime of some of us spoke of "the then mysterious fungi."

Science is not the accumulation of facts even of related facts, but the relating of observed facts to general principles. In this sense can we fix a time for the birth of the Science of Mycology?

In 1821 Elias Fries used the word "mycologia" in the first sentence of his classic three-volume *Systema Mycologicum*. In 1836 the Rev. Miles Berkeley wrote about Mycology but in 1860 he published a useful book of 400 pages with the hybrid title "Outlines of British Fungology." Doubtless he intended it to be a popular treatise and feared that the intelligent general public would not look into a book on Mycology. In his history of British Botany Reynolds Green makes the statement that British Mycology dates from the publication of Berkeley's Introduction to Cryptogamic Botany in 1857, "the first comprehensive treatment of the subject in any language." By Marshall Ward the honor of putting Mycology in the circle of

sciences is awarded to Anton de Bary whom he ranks the first of 19th century biologists and who will "always be remembered as the founder of the science of Mycology." Presumably he would date the laying of the foundation in the year of the publication of de Bary's "Morphologie und Physiologie der Pilze," 1866. The scientific study of fungi began about the middle of the last century and since then has become the parent of Bacteriology, Uredinology and other sub-sciences.

Returning to the conversation mentioned on a previous page, my acquaintance asked "What is Mycology, anyway?" I told him that it is the study of fungi. He revealed his opinion that fungi are mushrooms and toadstools and that there could not be much to talk about unless it is the troubles that people have who try to grow them in their cellars. He seemed surprised and interested as I stated some facts relative to the classification-range of fungi and the importance of their study.

The "mushrooms and toadstools," instead of being few kinds, number in the thousands and yet their names occupy but small space in the list of known species of fungi. Not many kinds are sought or cultivated for food and even their cultivation is not a negligible industry. There are canneries near the markets of the large eastern cities that are daily, for more than half the year, turning tons of fungi into canned food. Alga-fungi usually called lichens are the staple food for great herds of reindeer during the long winters in the countries bordering the Arctic regions and in times of dearth have saved the human population from starvation. Certain species are indispensable or serviceable in the arts of baking, cheese-making, brewing and other industries. I have read that well over a thousand patents have been granted involving the use of fungi in one way or another. Students of agriculture and mycology have made lists of soil-fungi which very beneficially modify the soil for crop-production.

On the other hand, there are armies of fungus-enemies to human interests. Almost every plant cultivated by man or made use of by him has been damaged somewhere to a greater or less extent by parasitic fungi. The losses thus caused to cereal crops all the world over exceed estimation. The valuable American chestnut in the United States and Canada has been

destroyed; the elm and white pine will follow the chestnut unless the parasite peculiar to each is controlled; efficient control in such cases is difficult and expensive. Every history of Great Britain and the United States refers to the tragic story of the potato mildew in Ireland in 1847, which caused starvation of thousands of people and produced a long train of physically and politically evil effects.

Animal as well as plant life is subject to fungus parasitism. A member of this Society, Dr. Carroll Dodge, is the author of a large book of 900 pages devoted solely to the descriptions and effects of fungi causing diseases of mammals including mankind of course. The late Dr. Roland Thaxter, the first President of the American Mycological Society, published two monographs, one of them incompleted at the time of his lamented death, totalling 1,267 quarto pages of printed text and many hundreds of drawings, dealing only with fungi inhabiting insects. Saccardo's Sylloge Fungorum now in preparation of the 26th volume has already published over 67,000 descriptions of fungi. One may safely assert that Mycologists and Mycological Societies in America and elsewhere will not solve all the problems arising in the study of fungi during this century.

Apart from attention to fungi for academic or vocational purposes they deserve notice from a recreational point of view. If my observation is of general application the commonest interest in fungus-hunting connects with anticipated pleasure at the supper table and the joy of telling the sympathetic neighbor all about the experience. Tripping over fields and in woods and peering into long grass and among weeds for a hoped-for fungus affords more variety and quite as much exhilaration as searching for a lost golf ball. Even if the collector returns with a light basket she usually has had "a good time." Observing and collecting all kinds of fungi and identifying them so far as possible from the available literature is a worth-while hobby. Most amateurs, who have about equal acquaintance with green plants and fungi in a recreational way, will say that fungi are the more interesting. Outdoors and in the working-room they make a greater challenge to effort. We all know people who have been kept awake too long over a cross-word puzzle. The identification

of a fungus may be no less gripping and unlike the word-puzzle it may not keep until the morning.

The three-day Summer Forays, organized by this Society, will be remembered with much pleasure by all those who had the good fortune to attend them. They afforded well-used opportunities for acquaintance-making of kindred spirits and association with them resulting in increased interest and advanced knowledge of the science. Hitherto these forays have been held at Cornell University, at Stewart's Camp at Seventh Lake in the Adirondacks, at the Biological Laboratory, Mountain Lake, Va., and at Dartmouth College, Hanover, N. H. In every case the local authorities left nothing undone to insure the success of the meetings.

For various reasons Mycology should be more widely known among the people and generally more highly appreciated. You who know this fact should pass on your knowledge. Seize opportunities that may come your way, or make them if you can, in organizing local clubs, contributing letters to the press or giving radio talks.

This year our official organ, MYCOLOGIA, brought 743 pages of good matter to its subscribers. Every member of the Society received a copy. The editor received contributions enough to increase the number of pages and some papers went elsewhere for lack of early accommodation. The typography and illustrations are all that can be desired; the size is necessarily limited to the available funds. By what means can the circulation and the revenue be increased? Can college and public library subscriptions be increased? Can publication rates be reduced without sacrifice of the present quality? Can some pages of more popular literature be introduced?

In the past, advertisements have not been admitted. SCIENCE, the official organ of the A. A. A. S., introduces valuable short articles in its renumbered, advertising pages. These articles unfortunately are not indexed. REVUE DE MYCOLOGIE—Annales de Cryptogamie Exotique—publishes a 16 page Supplement of more popular matter than the other papers which make up the body of the Review. If I am not mistaken the Supplement can be purchased separately. Publication-experiences of these and other similar journals may be worth considering.

After another year, and with more emphasis if possible, I close with the expression of the hope and confident expectation of my predecessor that the Mycological Society of America will increase its membership and its usefulness and that an enlarged MYCOLOGIA will reach and maintain preëminence among the mycological journals of the world.

LONDON, ONTARIO.

A NEW LIFE CYCLE INVOLVING CYST-FORMATION IN ALLOMYCES[1]

RALPH EMERSON

(WITH 11 FIGURES)

INTRODUCTION

Allomyces is a genus of aquatic fungi belonging to the small phycomycetous order Blastocladiales. *A. arbuscula,* the first species to be described, was discovered by Butler (**2**) in India. Other plants, subsequently isolated and studied by Barrett (**1**), Weston (**9**), and Coker and Grant (**4**), proved to be nearly identical with Butler's form. A second species, *A. moniliformis,* was isolated from soil at Smith Island, N. C., and in Haywood County, North Carolina, by Coker and Braxton (**3**). As described by them this fungus did not differ essentially from *A. arbuscula.* It was distinguished primarily by more elongate sporangia and by the fact that secondary zoösporangia were borne in unusually long chains.

Sexual reproduction was unknown in *Allomyces* until 1929 when Kniep described the gametophyte stage of a third species, *A. javanicus,* which he collected in Java. In this form Kniep (**7, 8**) discovered a regular alternation of equal sporophyte and gametophyte generations. Sporophyte plants bore thin-walled zoösporangia and reproduced asexually in the usual way by zoöspores from these sporangia. They also bore thick-walled, brown, pitted resistant sporangia. In these two reproductive features then and in general morphology also, *A. javanicus* was essentially similar to *A. arbuscula* and, for that matter, to *A. moniliformis* as well. Kniep found, however, that in *A. javanicus, monoecious gametophyte plants developed from R.S. zoöspores* (*i.e.* zoöspores from

[1] Contribution from the Cryptogamic Laboratories of Harvard University No. 153.

resistant sporangia)[2] *and bore male and female gametangia.* Uniflagellate, anisogamous planogametes emerged from these gametangia and fused in pairs to form biflagellate planozygotes. The latter, in turn, germinated directly and gave rise to sporophyte plants thus completing the cycle. Hatch's report (**6**) of sexuality and a similar alternation of generations in *A. arbuscula* fully confirmed Kniep's discoveries.

For comparative study and purposes of experiment the writer has isolated thirty strains of *Allomyces* from soil collected in a variety of localities in both hemispheres. He has found that, although a majority of these forms have a life cycle exactly the same as that described by Kniep and Hatch, four of them do not conform to such a scheme. They have *a strikingly different life history, distinguishing them markedly from all species of Allomyces,* such as *A. javanicus* and *A. arbuscula, which have a conspicuous alternation of sporophyte and gametophyte generations.* The distinctively different life cycle represented by these four isolates is described in the present paper.

ISOLATES AND METHODS OF CULTURE

The isolates which differed in this manner were obtained from the following soil samples:

Isolate	Soil from
(1) Burma 1B	Rangoon, Burma
(2) Venezuela 1	Barrancas, Venezuela
(3) China 2H	Hupeh, China
(4) China 2J	Hupeh, China

Burma 1B was used for all detailed studies of development because resistant sporangia of this isolate germinated with great readiness and uniformity in one or two hours when removed from agar cultures (two to six weeks old) and placed directly in water. Resistant sporangia of isolates (2) and (3) also germinated quite readily but those of China 2J could usually be induced to discharge spores only after they had been dried for a period of several days to a few weeks. The writer has begun a comparative study

[2] Throughout this paper the term "R.S. zoöspores" will be used to designate swarmers from resistant sporangia, whereas swarmers from thin-walled zoösporangia will be spoken of merely as zoöspores.

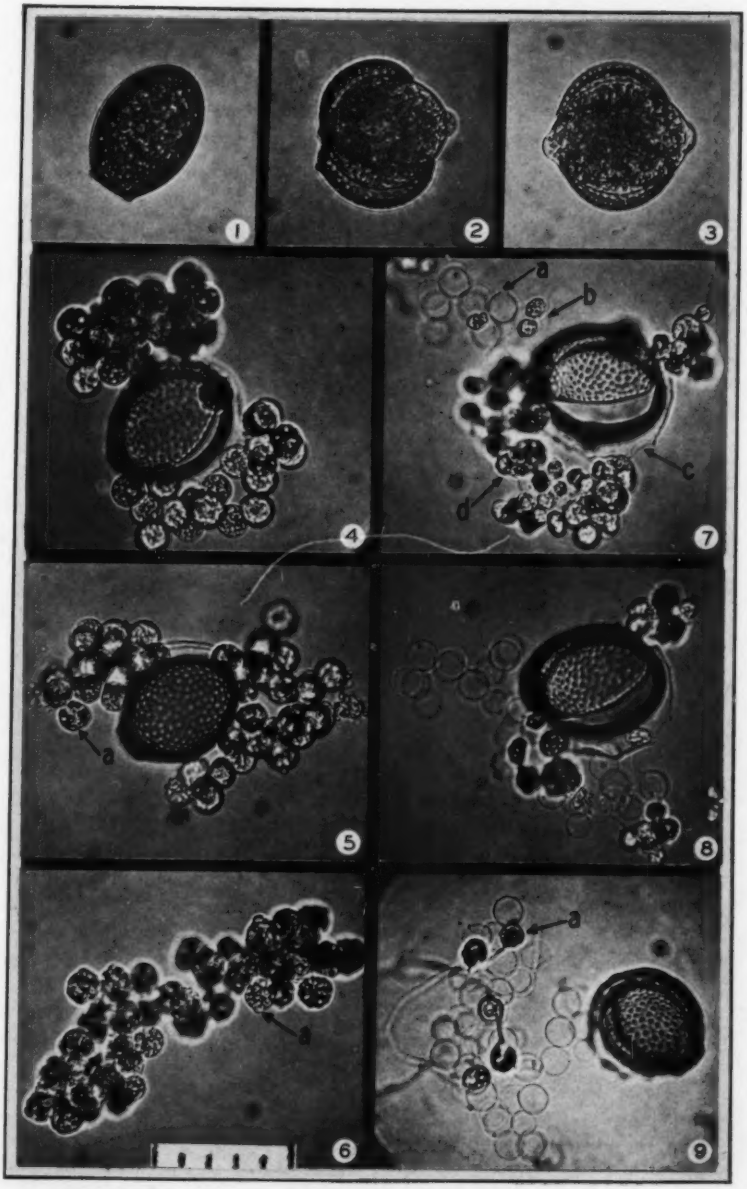
of the germination of resistant sporangia of different isolates in an attempt to discover why some appear to require a period of rest or maturation before they can be made to germinate, while others do not.

The fungi were grown in pure culture on a medium composed of 0.4 per cent Difco powdered yeast extract, 1.5 per cent soluble starch, 0.1 per cent K_2HPO_4 and 0.05 per cent $MgSO_4$, solidified with 2.0 per cent agar. Vigorous mycelia developed on this substratum and produced large numbers of zoösporangia and resistant sporangia. For comparative morphological studies plants were grown in a more normal environment on one or two boiled hemp seeds in 150–200 cc. of water. (Methods of isolation, culture and so forth will be described in detail in a monographic study of the genus which the writer is now completing.)

NEW LIFE CYCLE INVOLVING CYST FORMATION

Plants of the four isolates listed just above bore zoösporangia and resistant sporangia and were morphologically very similar to sporophytes of other strains. Thus the writer expected their R.S. zoöspores to put out germ tubes in the usual way and give rise to sexual individuals bearing gametangia. In the course of attempts

FIGS. 1–9. Cyst-forming *Allomyces* (isolate Burma 1B): Stages in resistant sporangium germination, encystment of R.S. zoöspores, and emergence of zoöspores from the cysts. Photomicrographs of living material. Approximately × 420 as here reproduced; each division of the scale in figure six represents 10 μ. 1, resistant sporangium which has just been removed from agar culture and placed in water; 2, germinating resistant sporangium one to two hours later; note that the heavy outer wall has split in the usual way, allowing the content to expand surrounded by the thin inner membrane; a single exit papilla has been formed; 3, similar to figure two but showing two exit papillae; 4, about 30 minutes later; germinated resistant sporangium with surrounding cluster of recently discharged and encysted R.S. zoöspores; 5, about one hour later cleavage planes are beginning to appear in the cysts as indicated at (*a*); 6, cluster of cysts about the same age as in figure five; note exit papilla on cyst at (*a*); 7, five to ten minutes later; zoöspores emerging from cysts; note (*a*) empty cyst showing exit pore, (*b*) zoöspores from cyst, (*c*) exit pore through which R.S. zoöspores escaped from inner membrane of resistant sporangium, (*d*) cyst showing cleavage planes in tripartite arrangement just before zoöspore discharge; 8, the same cluster of cysts three minutes later; note how all cysts from a single resistant sporangium discharge zoöspores almost simultaneously; 9, several hours later; a cluster of empty cysts and five cyst-produced zoöspores (one indicated at *a*) germinating with germ tubes.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to obtain this supposed gametophyte generation resistant sporangia were germinated and spore discharge was carefully studied. Observations soon revealed that although germination took place in the manner characteristic of all species of *Allomyces* (FIG. 2, 3), the emerging R.S. zoöspores were very sluggish and settled down in the immediate vicinity of the parent sporangia instead of moving actively away. In no case did they swim far or swarm for more than a few minutes. Studies of living as well as fixed and stained material (killed with osmic acid fumes and stained with 0.1–0.2 per cent aqueous gentian violet) showed beyond question that *the R.S. spores were characteristically biflagellate rather than uniflagellate as in other forms* (see discussion below). The flagella disappeared as soon as the swarmers came to rest and clusters of rounded and quiescent spores were to be seen around each emptied resistant sporangium (FIG. 4, 10, *A*).

These spores, however, did not proceed to put out germ tubes; on the contrary every one remained in a state of encystment for a period of about two hours. At the end of this time each cyst, as these structures may well be termed, had formed a single, small, characteristic papilla dehiscence (FIG. 6, *a;* 10, *B*). Lines of cleavage were also becoming apparent in the cysts, occasionally clearly dividing the content of one of them in a tripartite manner as shown in figure 10, *B*. Within two to five minutes after the clevage planes had become evident in living material the exit papillae opened and each cyst, functioning as a small sporangium, liberated several, small, posteriorly uniflagellate swarmers (FIG. 7, 8, 10, *D*). *These zoöspores which emerged never showed any indications of gametic fusion.* They swam actively, often for several hours, and finally settled down and germinated in the usual way by putting out germ tubes (FIG. 9). *The germlings thus formed did not develop into sexual plants bearing gametangia but, on the contrary, produced individuals just like their immediate parent. Thus, clearly, there was only one obvious generation in the life cycle and plants bearing distinctly different male and female organs were not formed.*

The process of cyst-formation with subsequent discharge of zoöspores was repeatedly observed in the four isolates listed above and there is no doubt whatever that the cysts represent a con-

stant and regularly recurrent stage in the normal life history of these plants. Even when observations were not made until some time after emergence of zoöspores from the cysts, a careful examination always revealed clusters of empty cyst walls scattered about near the germinated resistant sporangia (FIG. 9, 10, *D*).

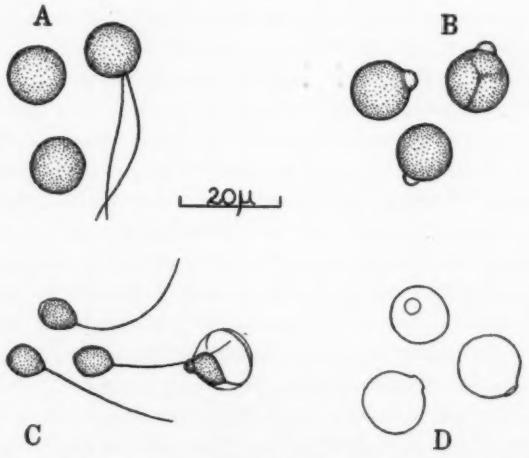

FIG. 10. Formation of cysts and discharge of zoöspores therefrom in *Allomyces* subgenus *Cystogenes*. Camera lucida drawings of isolate Burma 1B. Approximately × 750 as here reproduced. *A*, R.S. zoöspores; one rounded up but still retaining its two flagella, the others completely encysted. *B*, cysts shortly before discharging zoöspores; note the single obvious exit papilla on each, and also the tripartite cleavage planes shown in the upper one. *C*, quartet of zoöspores emerging from a cyst. *D*, empty cysts showing exit pores.

DISCUSSION

Two matters are of particular interest because of the bearing they may have on a possible interpretation of the life cycle which has just been described. The unusual and distinctive biflagellate condition of the R.S. zoöspores must be emphasized first. Cotner (**5**) showed that oversize, multiflagellate zoöspores were sometimes formed as a result of incomplete cleavage in the zoösporangia of *A. arbuscula* but that the normal small spores were always uniflagellate. From Kniep's studies (**8**) it was clear that swarmers from resistant sporangia of *A. javanicus*, like those from zoöspo-

rangia, were also typically uniflagellate. The writer's own observations have verified the fact that R.S. zoöspores—as well as other swarmers—of *A. arbuscula, A. javanicus* and all forms of *Allomyces* with a similar life cycle normally have but one flagellum.

In the writer's four isolates which form cysts, zoöspores from thin-walled zoösporangia are typically uniflagellate and similar in structure and behavior to zoöspores of all other isolates. The zoöspores derived from the cysts, though markedly smaller, are likewise uniflagellate. Bi- or triflagellate swarmers of either type occasionally appear but they are to be interpreted as cases of incomplete cleavage. In the cyst forming isolates, however, the R.S. zoöspores themselves, as was mentioned above, *regularly* have two flagella. This biflagellate character is so constant that the writer feels certain it is inherent and fundamental and does not result in this case merely from incomplete cleavage in the resistant sporangia. The R.S. zoöspores of cyst-forming isolates, therefore, show certain obvious similarities to the planozygotes produced by fusion of planogametes in *A. javanicus* and *A. arbuscula:* both structures are biflagellate and are, in fact, the only biflagellate spores to be found in their respective life cycles; both are sluggish and become quiescent after a very short period of motility.

The second point of special interest concerns the number of zoöspores which emerge from each cyst. The tripartite arrangement of cleavage planes sometimes seen in the cysts (FIG. 10, *B*) suggested that the zoöspores were, perhaps, being formed in quartets. To test this possibility cysts were picked out with capillary pipettes under a dissecting microscope and isolated singly in small hanging drops of water. Here they were kept under observation and the zoöspores emerging from each were counted. *A great majority of the cysts thus isolated, indeed 90 per cent of them, released four swarmers each.* Occasionally large cysts produced five, six, or more often eight swarmers. It was clear, however, that most of the zoöspores were emerging in groups of four.

Obviously the question, Of what significance are the cysts in the new life cycle which has been described?, must be considered. In as much as the writer has not yet made a cytological study of cyst formation or any other stages in the life cycle he cannot definitely answer this question now. Perhaps the formation of

cysts and the subsequent discharge of zoöspores is a purely asexual process. However, the results of the foregoing experimental and morphological studies point rather to the possibility that sexual fusions and subsequent reduction divisions are embodied in the cyst-forming life cycle. Thus the failure of cyst-derived zoöspores to behave as gametes, coupled with the strong resemblance which exists between planozygotes of *A. javanicus* or *A. arbuscula* and R.S. zoöspores of cyst-forming isolates, suggests that karyogamy may occur in the resistant sporangia of the latter at the time of germination or just previous thereto. R.S. zoöspores of cyst-producing isolates may, then, be zygotes; the formation of quartets of zoöspores in the cysts may be evidence that reduction divisions take place in these cysts. By means of cytological studies the writer hopes to ascertain whether the foregoing hypothesis is valid. It will be most interesting to see what relation there may be between the life cycle of species such as *A. javanicus* and that of the cyst-forming isolates.

RELATIONSHIP

Coker and Braxton (**3**, p. 139) reported that they had not seen germination of resistant sporangia in *A. moniliformis*. However, the writer was able to germinate resistant sporangia taken directly from agar cultures (see methods above) derived from a stock culture of this species very kindly sent from Chapel Hill, North Carolina, by Dr. John N. Couch. The writer found that *A. moniliformis produced cysts from R.S. zoöspores and had, in fact, a life history precisely the same as that of Burma 1B and the other three cyst-forming strains* listed above.

Coker and Braxton (**3**, *pl. 10, fig. 5*) figured structures which they described in their explanation of plates (**3**, p. 148) as follows: "Spores, showing one encysted within the sporangium and one escaping from cyst." They made no mention of these structures in the text but stated specifically in the description of *A. moniliformis* (**3**, p. 139), that zoöspores were monoplanetic. There is, therefore, a contradiction between the text and the figure, for zoöspores, apparently from a thin-walled sporangium, are shown encysted and giving rise to secondary zoöspores, *i.e.* as if illustrating diplanetism. Yet diplanetism has never been reported by any of the workers who have studied *Allomyces*, and the writer

has never observed encystment of zoöspores (from thin-walled sporangia) with subsequent formation of secondary swarmers in *A. moniliformis* or any of his own isolates. The writer has found, however, that R.S. zoöspores of *A. moniliformis* do encyst and it seems very probable, therefore, that the cysts which Coker and Braxton observed were not encysted zoöspores from thin-walled zoösporangia, as they were figured, but rather cysts formed by R.S. zoöspores from a resistant sporangium which had germinated in the vicinity.

Certain small morphological differences between the writer's cyst-forming isolates and *A. moniliformis* have been noted but further comparative study is being made to ascertain whether these differences are sufficiently constant to be of specific value. At any rate it is evident that all the cyst-producing forms discovered thus far are very closely related. The writer is of the opinion, therefore, that the new life cycle characteristic of his isolates and *A. moniliformis* is sufficiently distinctive and fundamental to warrant a tentative subdivision of the genus *Allomyces* into two subgenera as follows:

Subgenus 1. *Euallomyces*—including *A. javanicus* Kniep, *A. arbuscula* Butler, and all other forms having a similar life cycle.

Subgenus 2. *Cystogenes*—including the present four isolates, *A. moniliformis* Coker and Braxton, and all other forms having a similar life cycle.

A tabular comparison of these two subgenera is given below. Sporophyte individuals of *Euallomyces* are morphologically so similar to plants of *Cystogenes* that the certain identification of any undetermined isolate must depend on the type of life cycle which it is found to possess. Certain additional small, but characteristic differences between the two subgenera have been noted, however, and will be of value in tentatively placing new isolates in one subgenus or the other. Thus the resistant sporangia of all cyst producing forms have more conspicuous and widely spaced pits than do those of species included in *Euallomyces*. This difference is clearly shown in figure 11. Furthermore, members of the subgenus *Cystogenes* shed their mature resistant sporangia in

COMPARISON OF THE SUBGENERA EUALLOMYCES AND CYSTOGENES

Euallomyces	*Cystogenes*
(1) Obvious morphological alternation of equal sporophyte and gametophyte generations: sporophyte plants bear zoösporangia and resistant sporangia; gametophyte plants bear gametangia.	(1) No obvious morphological alternation of generations: plants bear zoösporangia and resistant sporangia.
(2) R.S. zoöspores: uniflagellate, active, often remain motile for a considerable time, germinate directly by a tube and give rise to gametophyte plants.	(2) R.S. zoöspores: biflagellate, sluggish, never remain motile for more than a few minutes, encyst and function as small zoöspores usually in groups of four. Cyst derived zoöspores uniflagellate, active, swarm and germinate in the usual way by a tube and give rise to plants like the immediate parent.
(3) Resistant sporangia: with fine closely spaced pits; not usually deciduous.	(3) Resistant sporangia: with obvious large pits more widely spaced; often strikingly deciduous, slipping from the outer sheath.

great numbers through splits in the outer, encasing sheath. In species of *Euallomyces* resistant sporangia are, it is true, sometimes released in this manner but they are much more apt to remain attached to the parent hyphae.

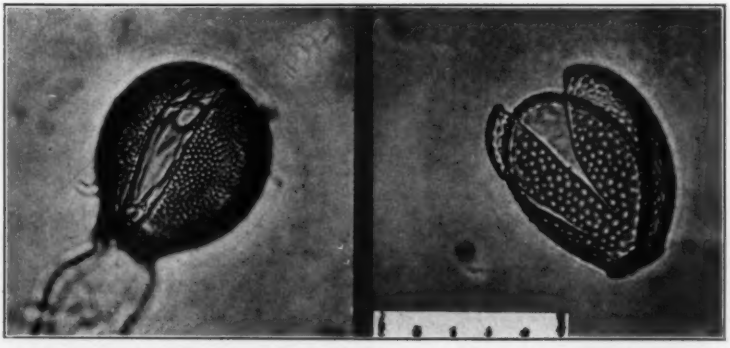

FIG. 11. A comparison of the type of pitting found in the walls of resistant sporangia of *Allomyces:* left, subgenus *Euallomyces* (*A. arbuscula* Butler, Weston's isolate from the Philippine Islands); right, subgenus *Cystogenes* (writer's isolate Burma 1B). Photomicrographs of germinated resistant sporangia, both approximately × 560 as here reproduced; each division of the scale represents 10 μ.

SUMMARY

1. For purposes of experiment and comparative study, thirty strains of *Allomyces* have been isolated from soil samples sent from various parts of the world. A majority of these isolates have a life cycle such as Kniep described in *A. javanicus* and Hatch subsequently found in *A. arbuscula*.

2. Four of the isolates, however, have a strikingly different life cycle: Zoöspores from resistant sporangia of these isolates do not germinate directly to produce gametophyte plants but, on the contrary, encyst immediately after their emergence. In the course of about two hours each cyst thus produced forms a single exit papilla and soon releases several (usually four) small, posteriorly uniflagellate zoöspores. The latter, after a swarm period, germinate to produce plants like their immediate parent. Hence there is only one obvious generation in this life cycle and it is composed of plants which, like the sporophytes of *A. javanicus* and *A. arbuscula*, bear thin-walled zoösporangia and heavy-walled resistant sporangia.

3. Zoöspores from resistant sporangia of cyst-forming isolates are biflagellate rather than uniflagellate as in other forms. They are very sluggish and swarm for only a few minutes. In these respects they resemble the planozygotes of *A. javanicus* and *A. arbuscula*.

4. A large majority of the cysts produce zoöspores in quartets. These zoöspores show no signs of gametic fusion.

5. The writer suggests the hypothesis that biflagellate zoöspores from resistant sporangia of cyst-forming isolates are actually zygotes, that sexual fusion takes place in the resistant sporangia at the time of or just before germination of the latter, and that reduction divisions occur in the cysts. This hypothesis will have to be tested by cytological studies.

6. Germination of resistant sporangia of *A. moniliformis*, reported for the first time, shows that the latter species produces cysts and has a life cycle exactly similar to that of the writer's four cyst-forming isolates.

7. The genus *Allomyces* is divided into two subgenera: *Euallomyces* to include all forms with a regular alternation of obvious sporophyte and gametophyte generations; *Cystogenes* to include

all forms producing cysts and lacking an obvious alternation of generations.

8. Secondary characters which may be used to distinguish members of the subgenus *Cystogenes* are (*a*) prominence and wide spacing of the pits in the walls of the resistant sporangia and (*b*) marked shedding of resistant sporangia at maturity.[3]

In conclusion, the writer is deeply grateful to Professor Wm. H. Weston, Jr., for his unfailing guidance and encouragement throughout the course of this work which was carried on under his direction. The writer is also most appreciative of the stimulating criticism and many helpful suggestions which he has received from Dr. David H. Linder.

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[3] Since the completion of this paper the writer has read with great interest Dr. Sörgel's recent report of investigations on the alternation of generations in *Allomyces*. (Sörgel, Georg. 1937. Untersuchungen über den Generationswechsel von Allomyces. Zeits. Bot. **31**: 401–446.) The writer wishes to point out that occasional departures from the normal life-cycle in *Euallomyces*, such as Sörgel has described, are not to be confused with the regularly recurrent cycle which is characteristic of *Cystogenes*. Sörgel has found (p. 409) that in the species he studied (belonging to the writer's subgenus *Euallomyces*), the zoöspores from resistant sporangia sometimes give rise directly to sporophyte rather than gametophyte plants. The writer, likewise, has noted that in certain strains of *Allomyces arbuscula* (of *Euallomyces*) sporophyte plants may develop from the resistant sporangial zoöspores. In such cases, however, the resistant sporangial zoöspores are not characteristically biciliate; they germinate by a tube in the usual way and never form cysts or give rise to secondary zoöspores. Clearly this is in marked contrast to the structure and behavior of the zoöspores from resistant sporangia in *Cystogenes*.

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MATERIAL FOR DEMONSTRATING THE ESSENTIAL FEATURES OF A BASIDIOMYCETE

B. O. Dodge

(with 2 figures)

Species of *Neurospora* are very adaptable for class demonstration of sexuality, life histories and Mendelian inheritance in ascomycetes. Biology teachers need comparable material for illustrating basidiomycetes.

During the summer of 1932, members of the Department of Dermatology, P. & S., Columbia University, studying the fungi arising on plates exposed in rooms where patients were suspected of having contracted asthma or hay fever, isolated what appeared at first to be a good hyphomycetous species. The plate was evenly covered with " conidiophores " each bearing a crown of from three to seven spores. More careful examination, however, proved that the erect spore-bearing structures were really basidia, which invariably arose from clamps along the surface hyphae or from clamps in a more or less erect proliferating system. This fungus was not found to be the cause of asthma in any patient, but it has been kept in culture by the writer because of the ease with which it can be grown and the origin of basidia from clamps demonstrated.

In agar tubes the basidia may become compacted to form a very good hymenial layer in spots. When grown on pieces of wood in large test tubes, a well marked fruiting structure of the *Corticium* type frequently develops. Dr. Rhoda Benham informs me that she has used this species in her class in medical mycology at P. & S. with gratifying results. Each student was able to grow the fungus in culture and follow the development of basidia very readily. Such a method of presentation is bound to make a deep impression on the student as he can plainly see how a compacting of the erect basidia into a layer is made the basis for circumscribing the old group hymenomycetes.

Species of *Corticium* and related genera bearing an indefinite number of spores on their basidia have been described in the past, but I was not certain of the identity of our species until Rogers published his "Notes on the lower Basidiomycetes" (Univ. Iowa

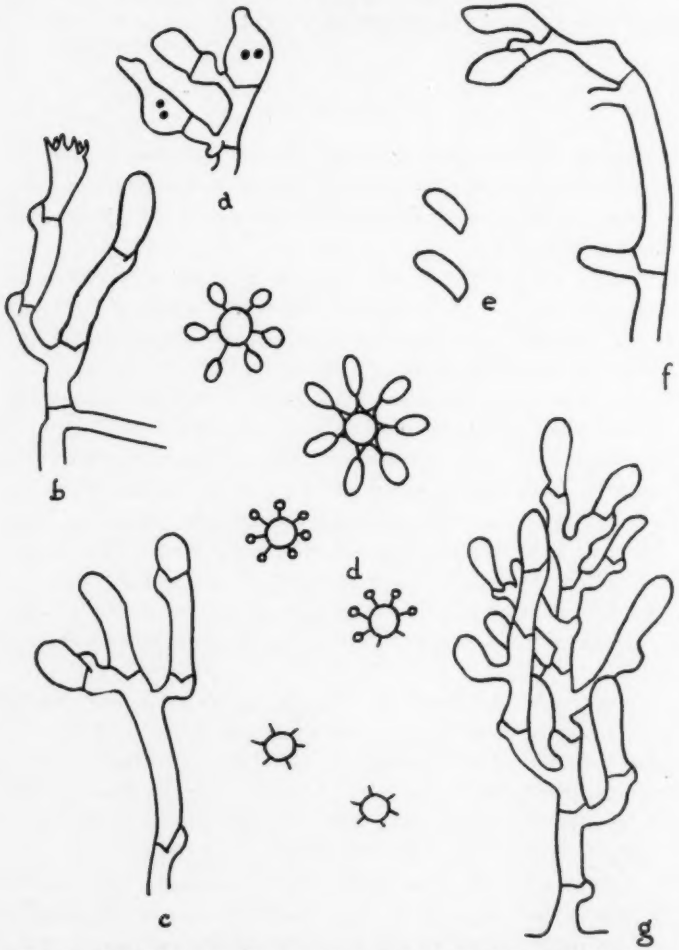

FIG. 1. *Corticium coronilla*. *a–c, f, g*, method of origin of basidia from clamp connections, *g* showing particularly well the proliferating system; *d*, optical sections looking down on basidia and showing various stages in development of spores at the crown; *e*, typical basidiospores.

Studies **17**: 1–43. 1935). Clearly our fungus is what he illustrates in his figure 11 and which he calls *Sistotrema coronilla* (Höhn) Donk. Cultures were sent to Dr. Rogers and he was able to con-

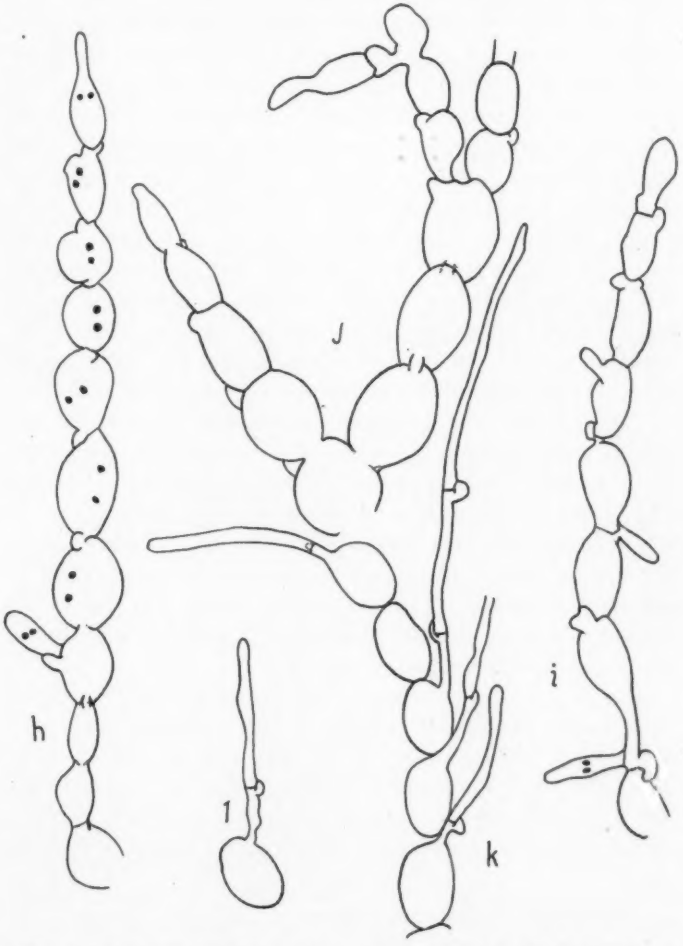

FIG. 2. *Corticium coronilla*. *h–j*, chains of brownish inflated bulbil-like cells developing at the surface in certain plate cultures. By focusing carefully one sees that adjacent cells are connected by clamps; *k*, *l*, germinating bulbil cells. Clamps are formed at once in germ tubes, whereas when single basidiospores are grown clamp formation is delayed for several days.

firm our identification. Figures illustrating certain characteristic morphological features and the way in which the basidia often arise in a system of proliferating clamp connections had been prepared in 1932 (FIG. 1, 2).

In 1936 Rogers gave us a very interesting account of "Basidial proliferation through clamp formation in a new species *Sebacina*" (Mycologia **28**: 347–362), making out that the clamp of basidiomycetes and the crosier of ascomycetes are homologous structures. We have recently been privileged to read a manuscript on "The species concept in *Corticium coronilla*," prepared by Miss R. Biggs [1] in Professor Jackson's laboratory at Toronto. Cultures of our fungus had been sent some years previously to Miss Nobles working in the same laboratory, but Miss Biggs does not mention having seen this material and no note of the culture is made in her manuscript. Our fungus falls in her Group II where the races are homothallic. We find the basidiospores 2.5–5 μ and the sterigmata $7 \times 3\ \mu$. The bulbil-like cells (FIG. 2) vary in size up to $8–10 \times 13–15\ \mu$ or more. Cultures from single spores invariably produce basidia although clamp formation may be delayed several days. Clamps are formed at once when the bulbil-like cells are germinated (FIG. 2, *k*). We have seen basidiospores with two nuclei in our material, but these may have been exceptions. Certainly the inflated bulbil cells in such chains as are shown in our figure 2, *h*, are often binucleate. This may be the reason why clamps are formed as soon as such cells germinate. The nuclear story should be studied more thoroughly in any case.

Miss Biggs is not yet ready to say that her groups I–IV represent distinct species. If one race is constantly heterothallic and the other is regularly homothallic, this ought to mark them as distinct species. In any event, because of the very fact that some are homothallic and others are heterothallic, we have in members of this *Corticium* (*Sistotrema*) complex excellent material for class use.

THE NEW YORK BOTANICAL GARDEN

[1] Mycologia **29**: 686–706. 1937.

NEW ZOOPAGACEAE CAPTURING AND CONSUMING SOIL AMOEBAE

CHARLES DRECHSLER

(WITH 4 FIGURES)

Four fungi that subsist by the capture of *Amoebae,* evidently to the exclusion of other nourishment, are described herein as new members of the Zoopagaceae. Though production of zygospores has been observed in only one of the species, the morphology of their vegetative and asexual reproductive parts establishes all four alike as undoubted members of the family, and, in addition, permits each to be distinguished from the several previously described forms congeneric with it.

ZOOPAGE MITOSPORA

A predacious species remarkable among conidial Phycomycetes for the length of its usually catenulate spores, was observed in two old maizemeal agar plate cultures started originally from pieces of tomato (*Lycopersicon esculentum* Mill.) roots found affected with cortical decay due to invasion by *Pythium ultimum* Trow. Two weeks after the plantings were made some pinches of leaf mold collected in deciduous woods on a mountain side near Cumberland, Md., in July 1935, had been added to one of the aging cultures; while the other had received similar additions of leaf mold gathered also in July 1935, in deciduous woods near Madison, Wis. In both cultures the fungus was present only in small quantity, being limited in each instance to a circular area of substratum about 15 mm. wide, adjacent to a deposit of the forest refuse. Its restricted extension and meager development within the areas occupied would seem to have been due to scarcity of the single species of *Amoeba* on which it subsisted. Captured specimens of the rhizopod in question showed a range in linear measurements from a minimum width of approximately 20 μ to a maximum length of about 70 μ, rounded individuals showing a variation in diameter between 25 μ

and 65 μ. Structures that appeared to be digestive vacuoles surrounding numbers of bacteria were often visible in the sarcode, as were also bodies of protozoan cysts, and, in a few instances (FIG. 1, *B*), thalli of some undetermined species of *Endocochlus* or *Cochlonema*. Though the protoplasm with its finely, dispersedly granular texture appeared fairly transparent, a nucleus could not be distinguished at all clearly in any of the captives, so that their identity remains, for the time being, uncertain.

In its predacious development the fungus shows most resemblance to *Stylopage areae* Drechsl. The relatively large lump of yellow adhesive material by means of which the animal is held fixed to the rangy mycelial filament, is traversed by a lateral outgrowth that penetrates the pellicle and then bifurcates several times at short intervals to give rise often to about a dozen basal branches (FIG. 1, *A, B*). These branches, for the most part distinctly narrower than the mycelial hypha from which they arise, traverse the protoplasm of the rhizopod in different directions until halted by the enveloping pellicle, sometimes giving off one or more ramifications in their courses. A rangy bushlike haustorial system is thus brought into being, which accomplishes the gradual exhaustion of the animal's substance (FIG. 1, *C; D; E, a*).

Asexual reproduction is most readily detected by examining the fungus under a dry objective without using a cover-glass, as the undisturbed conidial chains are easy to recognize by their erect posture. Even under low magnification the conidia arrest attention because of the considerable length frequently attained by them. Foreknowledge of their dimensions is desirable before a cover-glass is put on material selected for study, since under high magnification the conidia might otherwise be mistaken for segments of mycelial hyphae. In newly developed aerial elements the portions destined to become individual spores (FIG. 1, *F, b, c; G, h, i*) are set off from one another and from the supporting sterigmata (FIG. 1, *F, a; G, d*) by rather pronounced constrictions; wherefore the conidial extremities resulting from separation at the isthmi are characterized by marked tapering (FIG. 1, *E, c; G, f; H, a, b, c, d*), as are also the sterigmata, simple (FIG. 1, *E, b*) or branched (FIG. 1, *G, a–d*), that are easily recognized even after disarticulation has occurred. Similar tapering in a lateral arm borne on a conidium

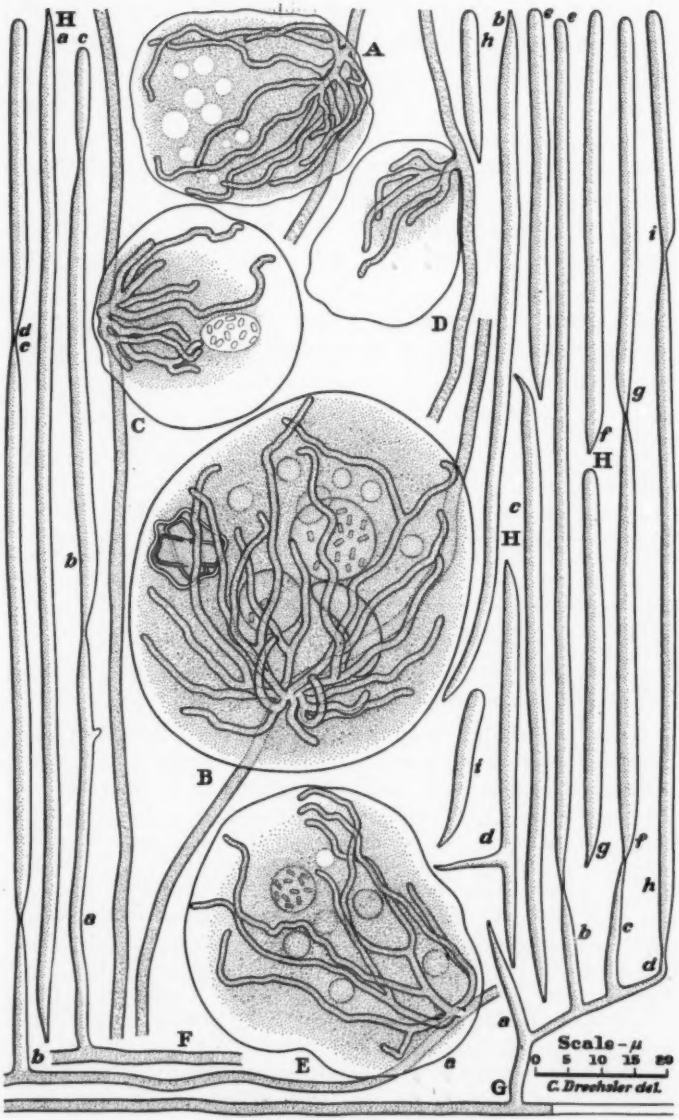

FIG. 1. *Zoopage mitospora.*

now and then (FIG. 1, *H, d*), gives evidence that the spore chains, though usually short, are at least occasionally branched. The distal end of each terminal conidium is distinguished by a bluntly rounded contour (FIG. 1, *E, d; G, g*) as in related catenulate forms. Owing to the small number of spores in a chain, and the replacement, occasionally, of a chain by a single long spore (FIG. 1, *G, e*), terminal conidia with rounded distal and tapering proximal ends (FIG. 1, *H, e, f, g, h, i*) are relatively much more abundant in the present fungus than in any congeneric species that has hitherto become known.

The shape of its conidium suggests for the fungus a specific name compounded from two words meaning " thread " and " seed " respectively.

Zoopage mitospora sp. nov.

Sparsa; hyphis hyalinis, pauciramosis, plus minusve recte positis, 1.5–2.5 μ crassis; haustoriis arbusculiformibus, 5–20 ramulis eorum divaricatis, irregulariter flexuosis, .7–1.4 μ crassis, usque 65 μ longis. Conidia levia, filiformia, interdum bifurcata, 22–156 μ longa, 1.6–3 μ crassa; in catenulas 2–5-sporas plus minusve erectas simplices vel pauciramosas digesta, vel interdum singulatim orta; deorsum semper attenuata, sursum magna ex parte attenuata, sed quandoque ultima in catenula vel singularia apice abrupte rotundata. Sterigmata similiter attenuata, saepe circa 20 μ longa, basi circa 2 μ crassa, simplicia vel paulo ramosa.

Amoebas usque 65 μ latas capiens et consumens habitat in humo silvarum, prope Madison, Wisconsin, et Cumberland, Maryland.

Sparse; vegetative hyphae hyaline, sparingly branched, usually following rather straightforward courses, 1.5 to 2.5 μ wide; haustoria bushlike, with close basal ramification and composed of 5 to 20 branches, mostly somewhat irregular in course, .7 to 1.4 μ wide and up to 65 μ long. Conidia smooth, filiform, sometimes bifurcate, 22 to 156 μ (average 83 μ) long and 1.6 to 3 μ (average 2.3 μ) wide; arising in more or less erect, simple or sparingly branched chains of 2 to 5 each, or sometimes borne singly; always tapering markedly toward the proximal end, and usually toward the distal end, but whenever solitary or borne terminally in a chain, having apex broadly rounded. Sterigmata similarly tapering, simple or occasionally branched, measuring usually about 20 μ in length and about 2 μ in basal diameter.

Occurring in leaf mold, subsisting on a species of *Amoeba* sometimes as much as 65 μ in diameter when rounded up, near Madison, Wis., and Cumberland, Md.

ZOOPAGE THAMNOSPIRA

A species of *Zoopage* remarkable for its extraordinary haustorial development, was observed in two maizemeal agar plate cultures 30 days after they had been started with pieces of decaying tissue from the roots and basal portion of the stem of a tomato plant found wilting in the greenhouse early in December 1935. The fungus subsisted apparently altogether on a species of *Amoeba* whose larger individuals measured approximately 40 μ in diameter when drawn into a more or less rounded shape. Each animal clearly revealed imbedded in its finely granular endoplasm a prolate ellipsoidal nucleus mostly 9 to 12 μ long and 6.5 to 8 μ wide, within which a dozen sphaeroidal bodies about 1.5 μ in diameter could be discerned, mostly in peripheral positions (FIG. 2, *A; B, a; C, a; F; G*). The smaller number and larger size of these nuclear inclusions, which probably represent chromatin bodies, offer some tangible basis for distinguishing the *Amoeba* here concerned from the one serving as prey for *Stylopage rhabdospora* Drechsl. (**6**), as well as from the apparently closely similar species habitually captured by *S. cephalote*.

Capture of the animals is accomplished, as in other members of the Zoopagaceae, by adhesion to a mycelial filament; the small lump of sticky substance effective in arresting each specimen remaining visible after perforation of the delicate pellicle as a yellow ring. Following penetration the invading hyphal branch grows some distance into the sarcode, usually widening markedly in its course, before branching dichotomously (FIG. 2, *A*). When the resulting thickish elements have attained a length usually of 10 to 30 μ, they may branch dichotomously (FIG. 2, *B, a, b; C, c, d*), whereupon renewed elongation and a third bifurcation may ensue in turn; so that in large animals a dichotomous system with 8 terminal elements is often present (FIG. 2, *C, b; D*). Spacial limitations, combined perhaps with continuing movements of the captive, become operative in constraining the rangy branches to grow in handsome curves rather than in straight lines.

The rather massive haustorium thus produced, through conforming to a design common to the homologous structures in various predacious members of the Zoopagaceae, is decidedly suggestive,

in its proportions and graceful coiling, of the vegetative thallus in the endoparasites referable to *Endocochlus* and *Cochlonema*. Apparently the endozoic development here is of an unusual and curious intermediate type, which finds, nevertheless, sufficient explanation in the instances of essentially parasitic infection observed in some number, where an adhering conidium thrusts a germ tube through an *Amoeba* (FIG. 2, *F, G*) to give rise inside to a coiled dichotomous branching system corresponding in the main to a *Cochlonema* thallus. In any case the endozoic apparatus gradually exhausts the protoplasmic materials of the animal (FIG. 2, *C, c–e*), and during the more advanced stages of such depletion becomes itself evacuated of protoplasm, often with the insertion of septa to mark the progress of withdrawal (FIG. 2, *B, b; C, f; E*).

Asexual reproduction takes place through the conversion of aerial filaments showing regularly spaced constrictions (FIG. 2, *H*) into chains of spores wherein verrucose fusoid conidia alternate with short and narrow empty connections (FIG. 2, *I*). As in other catenulate forms, the basal portions of the sporogenous hyphae are often little differentiated from the mycelial hyphae, neither exceeding the latter in width, nor being sculptured in any noticeable degree. These portions of sporogenous hyphae yield smooth, virtually filamentous spores markedly longer and narrower than the well differentiated conidia (FIG. 2, *L–O*) typical of the species, and somewhat longer and narrower than the numerous intergrading structures (FIG. 2, *J, K*) that are sparingly yet recognizably sculptured.

A term compounded from words meaning "bush" and "coil" respectively, and intended to be descriptive of the haustorium, is proposed as specific name for the fungus.

Zoopage thamnospira sp. nov.

Mycelium sparsum, pauciramosum; hyphis hyalinis, .8–1.6 μ crassis; haustoriis propter repetita incrementa 10–30 μ longa plerumque bis vel ter repetite dichotomis, ramis 2–3 μ crassis saepe in spiram laxum pulchre convolutis, itaque hyphae alitae specierum endoparasiticarum Zoopagacearum paulo similibus. Conidia typice minute sed distincte verrucosa, fusoidea, utrimque obtusa, 8–25 μ longa, 1.5–2.6 μ crassa, in catenulas saepe 10–15-sporas plus minusve erectas digesta. Zygosporae ignotae.

Amoebas magnam partem 20–40 μ longas capiens et consumens vel rarius easdem parasitice enecans, habitat in radicibus putrescentibus *Lycopersici esculenti* in viridario prope Beltsville, Maryland.

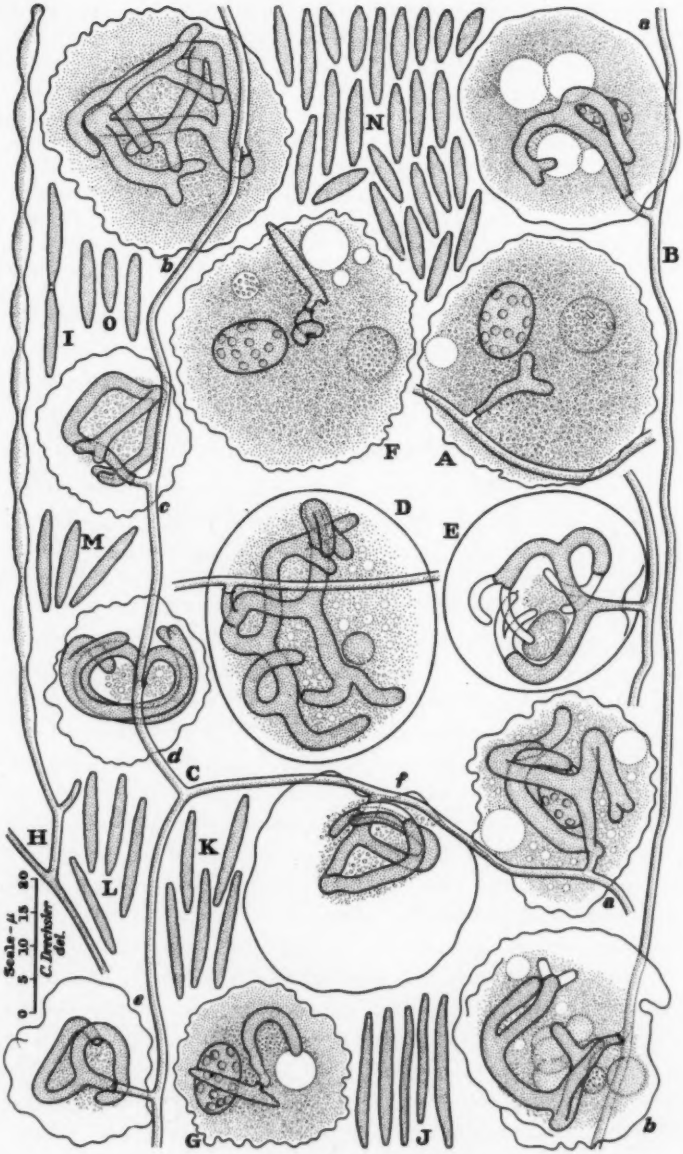

FIG. 2. *Zoopage thamnospira.*

Mycelium sparse, sparingly branched; hyphae hyaline, .8 to 1.6 μ wide; haustoria following repeated elongation by increments 10 to 30 μ in length, mostly bifurcating successively 2 or 3 times, the branches 2 to 3 μ wide, often handsomely convolved in loose spiral coils and thus resembling somewhat the vegetative hyphae in endoparasitic species of the Zoöpagaceae. Conidia sometimes filamentous, smooth, up to 40 μ in length and as little as 1 μ in width; but more frequently, and more typically, spindle-shaped, rounded at both ends, minutely yet distinctly verrucose, 8 to 25 μ (average 14 μ) long and 1.5 to 2.6 μ (average 2.1 μ) wide, and borne in more or less erect chains of 10 to 15 each. Zygospores unknown.

Capturing and consuming, or more rarely parasitically destroying a species of *Amoeba* mostly 20 to 40 μ in diameter; occurring in decaying roots of *Lycopersicon esculentum* in a greenhouse near Beltsville, Md.

STYLOPAGE CEPHALOTE

Early in May 1936, after indoor temperatures generally too high to permit good development of most members of the Zoopagaceae had been prevailing for some time, a handsome species of *Stylopage* made its appearance in an old maizemeal agar plate culture to which had been added earlier a few pinches of leaves partly decomposed in contact with the ground. Two months later the fungus again showed its ability to thrive at summer temperatures by developing spontaneously in an agar plate culture made in the isolation of *Pythium Butleri* Subr. from diseased portions of experimental spinach plants that were wilting and dying at Arlington, Va., evidently as the result of extensive decay in crown and taproot. In both cultures the fungus subsisted on an *Amoeba* rather closely similar to the species previously (**6**) found preyed upon by *S. rhabdospora* and then referred tentatively to *A. similis* Greeff. The dimensional relationships of the nuclei in the two species gave perhaps the clearest indication of difference in specific identity. Whereas the animals captured by *S. rhabdospora,* measuring mostly 30 to 40 μ in diameter, had an ellipsoidal nucleus 9 to 10 μ long and 7 to 8 μ wide, those captured by the fungus under consideration were each provided with a nucleus of similar prolate shape, 10 to 14.5 μ long and 7.5 to 8.5 μ wide. This large nucleus revealed close under its membrane approximately 30 darkish

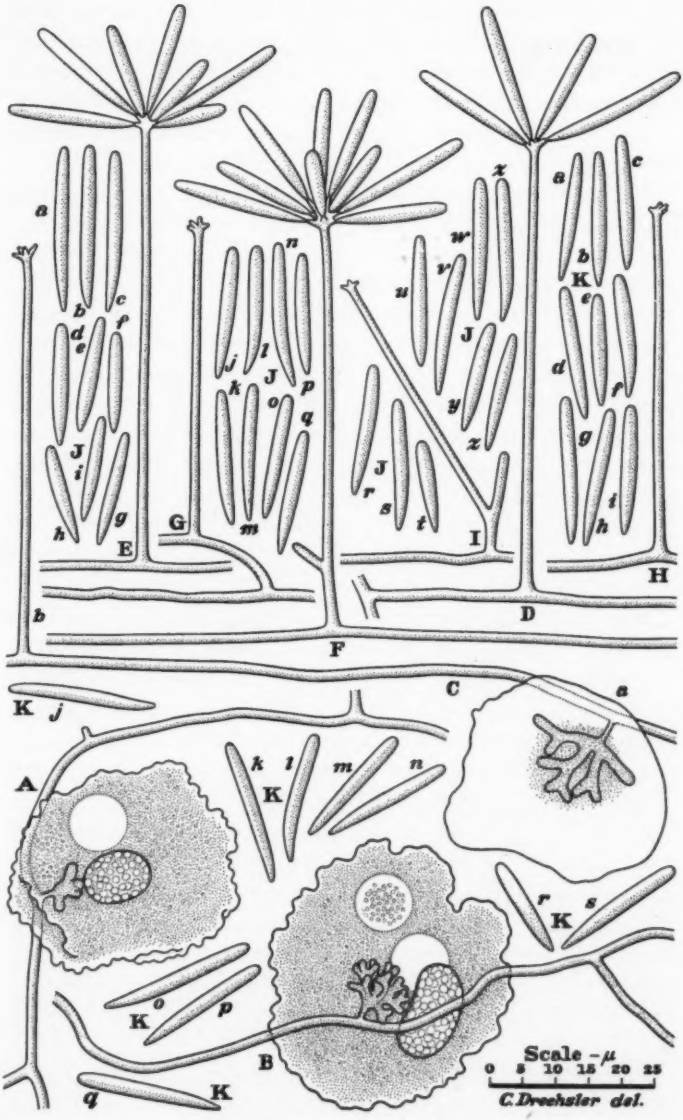

FIG. 3. *Stylopage cephalote.*

sphaeroidal bodies measuring about 1 to 1.2 μ in diameter, and distributed more or less evenly in a peripheral layer, wherein they maintained a continuous circulatory movement that was reminiscent somewhat of the movement of chloroplasts in epidermal cells of *Elodea* leaves, familiar from classroom demonstrations of cyclosis.

The mycelium of the fungus, like that of most predacious forms, is sparse. Yet branching would seem to occur here at closer intervals than in *Stylopage rhabdospora*, and the individual hyphae, while of the same width as the filaments of that species, often take courses with capricious curves and turns. Capture of a susceptible *Amoeba* by adhesion to a mycelial filament is promptly followed by perforation of the delicate pellicle and development of a haustorium (FIG. 3, *A;* 4, *A*), which through variation in the number and closeness of its bifurcations, may show in its definitive condition either an open (FIG. 3, *C, a;* 4, *B*) or a more compact (FIG. 3, *B*) arrangement of parts. After gradual appropriation both of the animal's finely granular cytoplasm and of its impressive nucleus, only the empty pellicle remains behind, to collapse and finally to disappear.

Asexual reproduction takes place somewhat more sparingly than might be expected from the number of animals consumed. The erect conidiophores (FIG. 3, *C, a; D–J*) that arise here and there from superficial hyphae, are of about the same stature as the more nearly medium-sized fertile hyphae of *Stylopage rhabdospora*. On them are borne in bristling capitate arrangement from 4 to 9 conidia decidedly smaller than the homologous structures of *S. rhabdospora*, but closely similar to those of *S. haploe* Drechsl. in shape and size (FIG. 3, *J, a–z; K, a–s*). The resulting aerial apparatus (FIG. 3, *D, E, F*) is of handsome appearance, modestly imitating, as it does, the beautiful habit of various nematode-capturing Hyphomycetes, as, for example, *Dactylaria candida* (Nees) Sacc.; the imitation furnishing another striking instance of convergence brought about evidently by a predacious mode of life.

Sexual apparatus is produced in moderate quantity, often through fusion of a mycelial branch with the germ tube of a fallen conidium (FIG. 4, *C, a–e*), so that confusion with homologous ap-

paratus of other members of the Zoopagaceae present in the same tract of substratum, is conveniently obviated. In such zygophoric germination of conidia, as in dimensions of conjugating elements, of zygosporangium and zygospore (FIG. 4, *C*, *f–h*), close similarity to *Stylopage rhabdospora* is again apparent.

Although the original definition of *Stylopage* does not make provision for a distinctly capitate arrangement of the conidia, the fungus is referred to that genus because of its obviously close relationship to *S. haploe* and *S. rhabdospora*. No emendation of the generic diagnosis is proposed at present, in view of the possibility that discovery of other capitate species may sooner or later make advisable the erection of a separate genus related to *Stylopage* in the same way as *Dactylaria* is related to *Dactylella* among the predacious Hyphomycetes. In the meantime a specific epithet meaning "headed" may aptly direct attention to the most striking characteristic of the fungus.

Stylopage cephalote sp. nov.

Sparsa; hyphis sterilibus incoloratis, 1.2–1.8 μ crassis, haustoria pedicellata evolventibus; pedicello saepius .6–.7 μ crasso, 2–4 μ longo, ramulis usque quater dichotomis, divaricatis, 1–2 μ crassis, usque 10 μ longis; hyphis fertilibus incoloratis, saepius 45–75 μ altis, basi 1.2–2 μ crassis, sursum paulatim attenuatis, apice 1.1–1.3 μ crassis, ibi 4–9 conidia in capitulum pulchrum radians digesta ferentibus. Conidia elongato-cylindracea, sursum abrupte rotundata, deorsum plerumque attenuata, basi acutiuscula, 14–25 μ longa, 1.8–25 μ lata. Zygosporangia primo levia, sphaeroidea, 8–10 μ diam., in maturitate membrana circa zygosporam collabente; zygospora flavida, sphaeroidea, 7–9 μ diam., membrana .7–1.8 μ crassa, 10–20 verrucis ornata.

Amoebas plerumque 25–35 μ latas capiens et consumens, habitat in radicibus putrescentibus *Spinaceae oleraceae* et in foliis semisepultis putrescentibus, in Arlington, Virginia, et prope Beltsville, Maryland.

Sparse; vegetative hyphae colorless, 1.2 to 1.8 μ wide, producing haustoria composed individually of a stalk mostly .6 to .7 μ wide and 2 to 4 μ long, together with branches bifurcating successively 2 to 4 times, and measuring 1 to 2 μ in width by 10 μ in length; fertile hyphae colorless, mostly 45 to 75 μ high, 1.2 to 2 μ wide at the base, gradually tapering to a width of 1.1 to 1.3 μ at the apex, where on short tapering projections 4 to 9 conidia are borne in bristling capitate arrangement. Conidium cylindrical, abruptly rounded at the apex, mostly tapering markedly toward the somewhat acute base, 14 to 25 μ (average 20 μ) long and 1.8 to 2.5 μ (average 2.2 μ) wide. Zygosporangium at first smooth, spherical,

8 to 10 μ in diameter, its wall at maturity collapsing about the zygospore; zygospore yellowish, subspherical, 7 to 9 μ in diameter, with a wall .7 to 1.8 μ thick, ornamented with 10 to 20 wartlike protuberances of which 6 to 8 are visible in the sigillate profile.

Occurring in decaying roots of *Spinacea oleracea* L., and in partly buried decaying leaves, capturing and consuming a species of *Amoeba* mostly from 25 to 35 μ in diameter, in Arlington, Va., and near Beltsville, Md.

ACAULOPAGE ACANTHOSPORA

In an old maizemeal agar plate culture to which some greenhouse refuse undergoing moist decomposition had previously been added, conidia of small dimensions but striking appearance were observed scattered sparsely over the surface of the substratum close to the deposits of decaying material. As an obvious similarity in general habit to *Acaulopage tetraceros* Drechsl. (3) was strongly suggestive of membership in the Zoopagaceae, a closer examination was made, with the result that the underlying mycelium was, indeed, found to be of the sparse, non-septate predacious type usual in this family. Though the rather delicate hyphae were in part superficial, in the main they followed their somewhat irregular courses under the surface of the agar. *Amoebae* in varying stages of depletion were found attached here and there both to the superficial and to the submerged filamentous elements (FIG. 4, *D–I; J, a*). Some of the captured animals gave no indication of their identity, except such as might be conveyed in moderate or small dimensions, a frequently elongate shape, and a relatively small nucleus, showing a darkish central globose body within a narrow lighter peripheral layer (FIG. 4, *D; F; G, a; I*). In addition to these features, other adhering specimens exhibited unmistakably a tuftlike group of minute digitations (FIG. 4, *H*), or a less crowded array of deltoid protuberances manifestly representing a cluster of digitations partly relaxed and in process of obliteration. The captured rhizopods were therefore readily referred to *Amoeba limax* Duj., of which species, in truth, numerous living individuals could still be seen moving on or through the substratum.

Since in locomotion *Amoeba limax* always carries its tuft of digitation in the rear, it might be expected that captured specimens

would nearly always be attached by a portion of pellicle diametrically opposite to it in position. Such, however, is not the case, for rather frequently the adhesion takes place in close proximity to the posterior tuft (FIG. 4, *E; G, b; H*), indicating that capture does not always result at once whenever contact occurs, but is influenced a good deal by the caprice of circumstance. In any case, following capture, the lateral branch thrust through the pellicle of the animal ramifies almost immediately upon reaching the interior to give rise to a few flexuous elements of approximately the same width as the mycelial hyphae. These haustorial elements gradually bring about the assimilation of the animal's substance, and during the later stages of depletion are themselves progressively evacuated of protoplasm (FIG. 4, *G, b; H; I*), much like the homologous structures in other members of the family.

The conidia of the fungus are formed singly flush on the surface of the substratum, in large part at least, on the up-curved tips of somewhat short, superficial or nearly superficial hyphal branches (FIG. 4, *J, b; K; L*). In the beginning they develop as smooth globose terminal bodies (FIG. 4, *J, b; K*); but on approaching definitive size, each proliferates from its distal hemisphere usually a dozen or more tapering digitiform protuberances (FIG. 4, *L*). These protuberances are some time later evacuated by the retreat of their protoplasmic contents, and thus converted into empty appendages (FIG. 4, *M–W*). In some conidia an empty basal stipe is present as a prolongation of the noticeable pedicellus (FIG. 4, *M, O, S, U*), duplicating the condition usual in *Acaulopage ceratospora* Drechsl. (**3**) and *A. tetraceros;* though, perhaps more frequently, no empty basal appendage is visible here (FIG. 4, *N, P, Q, R, T*) whether because of abortive development, or early collapse, or damage suffered during disarticulation. More constant characters decisively distinguishing the species from *A. tetraceros,* are, of course, represented in the distribution of the more numerous and smaller appendages generally over the distal hemisphere of the conidium instead of in an apical zone, and in the smaller volume and globose rather than inverted lageniform shape of the living cell.

It is intended to bring into relief the characteristic bristling appearance of the conidium in a name composed from words meaning "spine" and "seed" respectively.

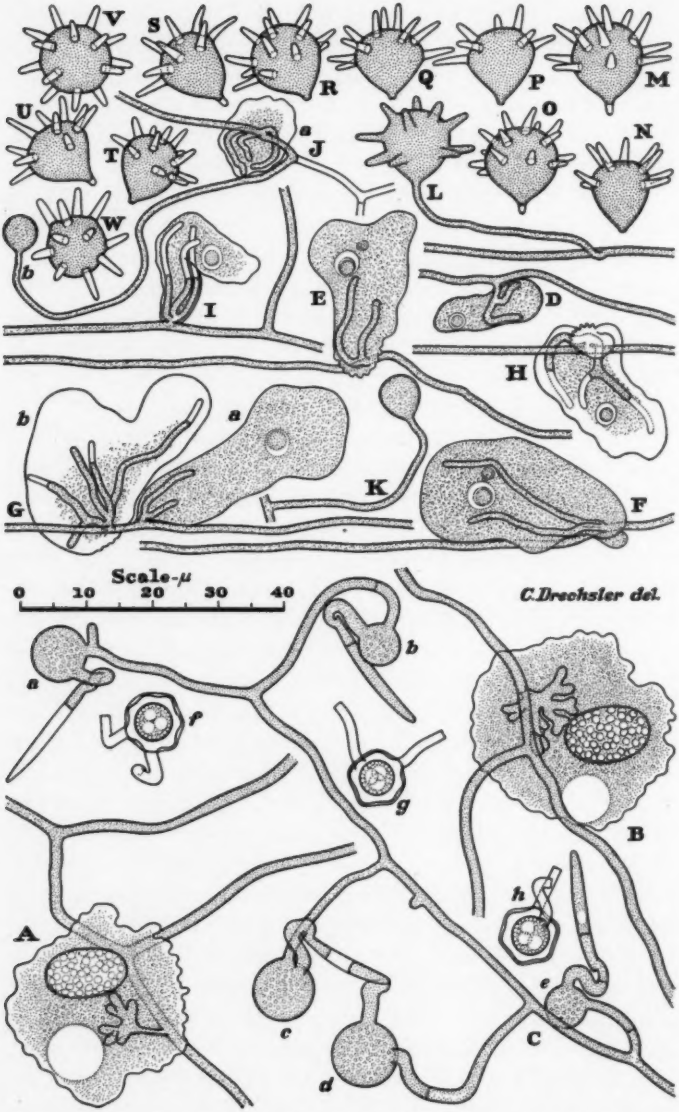

FIG. 4. *A–C, Stylopage cephalote; D–W, Acaulopage acanthospora.*

Acaulopage acanthospora sp. nov.

Sparsa; hyphis incoloratis, .7–1.4 μ crassis; haustoriis praecipue basi dichotomis, ex 2–4 ramulis flexuosis, 5–30 μ longis, 1–1.3 μ crassis compositis. Conidia hyalina, minute pedicellata; cellula viventi protoplasmatis repleta, globosa, interdum paulo applanata tum plus minusve turbinea, saepius 10–12 μ longa, 9–10.5 μ lata, in dimidio supero 7–18 appendicibus vacuis divergentibus digitiformibus, 3–6 μ longis, basi 1–2 μ crassis, sursum attenuatis, apice rotundatis praedita.

Amoebam limacem capiens et consumens, habitat in materiis plantarum putrescentibus, prope Beltsville, Maryland.

Sparse; hyphae colorless, .7 to 1.4 μ wide, producing haustoria mostly basally dichotomous and composed of 2 to 4 flexuous branches 5 to 30 μ long and 1 to 1.3 μ wide. Conidia hyaline, noticeably pedicellate; the single living cell of each, mostly globose but occasionally flattened into somewhat turbinate shape, in any case measuring 10 to 12 μ in length by 9 to 10.5 μ in transverse diameter, and bearing distributed over its distal hemisphere 7 to 18 empty divaricate slightly tapering digitate appendages measuring 3 to 6 μ in length and 1 to 2 μ in basal diameter.

Occurring in decaying plant remains, capturing and consuming *Amoeba limax*, near Beltsville, Md.

DEFINITION OF THE FAMILY

With the four fungi presented herein thirty species have been described in the Zoopagaceae. When the family was first proposed (**2**) a definition was intentionally postponed in the hope that discovery of additional members might reveal more adequately the scope of morphological diversity within the group, and at the same time supply clearer indications of the relationships to some of the older established taxonomic subdivisions in the Phycomycetes. The species found since then have, indeed, brought to light unexpected departures in vegetative and reproductive development, such as are embodied, for example, in the long filamentous conidium of *Zoopage mitospora*, in the curiously appendaged asexual spore of *Acaulopage acanthospora*, in the circinate thallus of *Cochlonema cylindricum* Dreschsl. (**7**), and in the dentate zygosporangium of *Z. odontosperma* Drechsl. (**7**). Somewhat surprisingly, too, the two tendencies in design of endozoic parts represented in the short thick spirally coiled vegetative hypha characteristic of most endoparasitic species, on the one hand, and in the divaricately branched

haustorium usual in predacious forms on the other (**3**), are largely reconciled when the moderately thickened and extensively coiled thallus of *C. megaspirema* Drechsl. (**7**) is considered in conjunction with the typically dichotomous, spirally disposed, swollen haustorium of *Z. thamnospira*.

Yet concerning the relationship of the Zoopagaceae to older groups within the Zygomycetes little additional information has been gained. Though asexual reproductive apparatus in all species of *Cochlonema* and *Zoopage* was carefully examined, nothing has been observed that could be held to argue in favor of endogenous development of the conidia in catenulate members of the family, or otherwise to sustain any supposition of homology between the conidial chains in these members and the rows of spores in the Piptocephalidaceae. Again, the rather initimately suggestive resemblance of *Stylopage hadra* Drechsl. to the insectivorous Entomophthoraceae (**2, 4**) has been found merely repeated without amplification in *S. leiohypha* Drechsl. (**5**).

While the Zoopagaceae show general similarity to the Entomophthoraceae in subsisting on living animals, and in reproducing asexually by conidia and sexually by zygospores, the differences between the two families are, nevertheless, very obvious. Of the thirty forms destructive to rhizopods and nematodes, not any shoot away their conidia or show the least adaptation for the violent discharge of spores that provides an outstanding characteristic of the older group. In visible habit, especially under natural conditions but to a marked degree even on transparent artificial culture media, the Zoopagaceae simulate the more delicate of the saprophytic molds; their conidial apparatus appearing sparsely distributed on the surface of the substratum in a manner certainly not at all reminiscent of the insectivorous Entomophthoraceae, nor, for that matter, of *Conidiobolus* or *Basidiobolus*, despite the effuse vegetative development usual in these two genera. Such scattered distribution is naturally to be expected in terricolous fungi living by the capture of microscopic animals that roam about in the decaying materials underneath; being, indeed, shared also by the predacious Hyphomycetes belonging mostly to the genera *Trichothecium, Arthrobotrys, Dactylella* and *Dactylaria*, when these develop under natural conditions. Much the same scattering of

conidial apparatus with concealment of biogenous relationship, prevails likewise among the endoparasitic and ectoparasitic members of the Zoopagaceae. As an infected host animal usually succumbs well under the surface of the substratum, the origin of the plural conidiiferous filaments is under natural conditions completely hidden from view; so that when these filaments emerge into the air at well separated points to extend themselves recumbently considerable distances in various directions and often to mingle with similar filaments from other sources, their common origin in a parasitized individual organism could hardly be suspected. Through the rangy disposition of sporiferous hyphae, the conidia formed from them are from the outset spread over a comparatively large area, and are thus given a better chance for encountering susceptible animals than would be provided by a closer arrangement. The relatively extensive development of the sparse mycelium in predacious members of the family, and the spindling aerial development in parasitic members, seem therefore to operate toward an end that is accomplished spectacularly in the Entomophthoraceae by the forcible discharge of conidia, and that perhaps is somehow promoted in the Harpellaceae by the helicoid spore appendages first described by Léger and Gauthier (**9**), and more recently figured for one species by Gauthier (**8**).

The rangy mycelial habit of the predacious forms offers a marked contrast to the compact vegetative habit shown by species of *Actinomyces* especially in liquid or agar or gelatin culture media. Yet the contrast may be less significant than conspicuous, possibly resulting from the exigencies of a predacious mode of obtaining nourishment as contrasted with a saprophytic or a parasitic mode. Certainly the thallus in the parasitic genera *Endocochlus* and *Cochlonema,* which during most of its growing period is everywhere immersed in food material, is not lacking in compactness. If pronounced thickening and spiral convolvement make this thallus look much different from the mycelium of *Actinomyces,* or of other groups of fungi, these modifications evidently are representative not so much of a fundamental morphological tendency in the family as of physical adaptation to life in a rather small animal with indeterminate rolling locomotion.

The production in *Cochlonema cylindricum* of relatively small

rod-like smooth conidia through segmentation of decidedly little differentiated aerial filaments, shows much similarity to spore formation in those species of *Actinomyces* that likewise have very simple conidial apparatus. Divergent tendencies in differentiation obscure this similarity in the more distinctive forms: verrucose sculpturing, unknown in *Actinomyces,* adding character to the conidia of many catenulate members of the Zoopagaceae; while elaborate coiling of aerial sporiferous branches, altogether alien to the Zoopagaceae, beautifies the conidial apparatus in numerous species of *Actinomyces.*

As the phycomycete with *Pythium*-like chlamydospores that in an earlier summary was figured synoptically (**1**: *p. 269, fig. 15; p. 270, lines 7–19*) among other fungi also predacious on nematodes, has not yet been definitely referred to the family under discussion, it is conveniently omitted from consideration in the diagnosis here submitted.

Zoopagaceae fam. nov.

Fungi plerumque minuti, terrestres, animalcula (Rhizopoda et Nematoda) enecantes. Mycelium specierum animalia capientium hyalinum, continuum, late effusum, irregulariter ramosum, haustorium ramosum in captum insinuans, hoc carnem illius exhauriens; hyphae alitae specierum intra animalia crescentium autem plerumque breves, crassae, simplices vel bifurcatae vel repetite dichotomae, saepius semel vel pluries spiraliter convolutae. Conidia hyalina, levia vel verrucosa, saepe filiformia vel fusoidea rarius globosa, interdum appendiculas vacuas praecipue sursum ferentia; nunc singulatim hinc illinc ex hyphis repentibus mycelii vel hyphis fertilibus arachnoideis recumbentibus assurgentia, nunc ex apice hypharum fertilium erectarum oriunda singularia vel in capitula laxa aggregata, nunc in catenulas plus minusve elongatas digesta; illa unius speciei cognitae ad animalia haerentia, haustorium intus evolventia, tum ipsa magnopere tumescentia. Zygosporangia saepissime in materia circum animalia vel sub animalibus raro intra animalia, ex copulatione hypharum similium orta, membrana modo zygosporam laxe circumdans, modo verisimiliter cum hac concreta.

Mostly minute terricolous fungi subsisting by the destruction of small animals (rhizopods and nematodes). Vegetative thallus in predacious species consisting of a hyaline, continuous, extensive, irregularly and rather sparsely ramifying mycelium, which gives rise to variously branched haustoria within the captured animals and by means of these haustoria appropriates the fleshy contents; in endoparasitic species consisting of a hypha, short,

thick, simple or bifurcate or repeatedly dichotomous, and, when well developed, wound spirally in a coil of one or more turns; in ectoparasitic species consisting of a swollen conidium adhering externally to the animal, together with the branching haustorium inside produced directly by germination of the conidium. Conidia aerial, hyaline, smooth or somewhat verrucose, mostly filiform or spindle-shaped though occasionally globose, sometimes bearing empty appendages in mainly distal positions; now arising laterally and singly at intervals from prostrate mycelial hyphae or from recumbent arachnoid sporiferous filaments; now budded off terminally one by one, or more nearly simultaneously and in loose heads, on approximately erect conidiophores; now produced in chains of variable lengths. Zygosporangium resulting from the conjugation of two similar hyphae, produced rarely within the animals attacked but much more frequently in the solid substratum surrounding or underlying them; its membrane at maturity in some species well separated from and loosely collapsed about the zygospore, in other species rather indistinguishably fused with the zygospore wall.

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EXPLANATION OF FIGURES

FIG. 1. *Zoopage mitospora;* drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout. *A,* Portion of hypha with a well developed haustorium in a relatively small captured *Amoeba. B,* Portion of hypha with an extensive haustorial system in a large captured *Amoeba;* within the animal are visible, in addition, an encysted organism, several digestive vacuoles, and a young thallus of an endoparasitic member of the Zoopagaceae. *C,* Portion of hypha with a small captured *Amoeba,* mostly depleted of protoplasm. *D,* Portion of hypha with a small captured *Amoeba,* whose contents have been almost wholly appropriated by means of the correspondingly small haustorium. *E,* Portion of hypha on which are borne a moderately extensive haustorium in the medium-size *Amoeba, a,* and at some distance a sterigma, *b,* with two catenated conidia, *c* and *d. F,* Portion of a superficial hypha with an erect sporogenous branch, wherein a basal portion, *a,* and two spore initials, *b* and *c,* are distinguishable. *G,* Portion of hypha with a branching sterigma: one spur, *a,* being denuded; a second, *b,* bearing a single long conidium, *e;* a third, *c,* bearing two catenated conidia, *f* and *g;* and a fourth, *d,* being continuous with the sporogenous filament consisting of the spore initials, *h* and *i. H,* Conidia, *a–i,* showing variations in size and shape.

FIG. 2. *Zoopage thamnospira;* drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout. *A,* Portion of hypha with a young haustorium in a captured *Amoeba,* within which is shown, besides, a small contractile vacuole, a spherical digestive vacuole and an ellipsoidal nucleus. *B,* Portion of hypha with a partly developed haustorium in a captured *Amoeba, a,* and a partly evacuated haustorium in the largely depleted *Amoeba, b. C,* Branched portion of mycelium on which are being held six captured *Amoebae* with protoplasmic contents in different stages of depletion, and occupied by haustoria variously developed. *D,* Portion of hypha that has given rise within a captured *Amoeba* to a well developed haustorium, which shows spiral curvature of the regularly dichotomous branches. *E,* Portion of hypha that has produced within a captured *Amoeba* a well developed haustorium with rather regularly dichotomous, handsomely curved branches; the distal branches having become evacuated with the approaching exhaustion of the captive's protoplasmic materials. *F,* A large *Amoeba* being invaded by a germ tube from an adhering conidium; a contractile vacuole, two digestive vacuoles, and the nucleus are visible within the animal. *G,* A smaller *Amoeba* similarly being invaded by the germ tube of an adhering conidium. *H,* Portion of a superficial hypha with an aerial conidiiferous filament. *I,* Two adjacent conidia in a mature chain, showing the empty connection between them. *J–O,* Conidia, showing variations in shape and size.

FIG. 3. *Stylopage cephalote;* drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout. *A,* Portion of hypha showing

a haustorium partly developed, within a captured *Amoeba;* in the animal is seen besides, a spherical contractile vacuole and an ellipsoidal nucleus. *B,* Portion of hypha with a well branched haustorium visible in a captured *Amoeba. C,* Portion of hypha on which have been produced a well developed haustorium within the almost wholly depleted *Amoeba, a,* and, some distance away, a conodiophore, *b,* now denuded of its spores. *D, E, F,* Conidiophores bearing four, seven and nine conidia respectively. *G, H, I,* Denuded conidiophores. *J, a–z; K, a–s,* Conidia, showing variations in size and shape.

FIG. 4. Drawn with the aid of a camera lucida at a uniform magnification; × 1000 throughout.

A–C, Stylopage cephalote: A, B, Portions of mycelium, each with a partly developed haustorium inside of a captured *Amoeba;* within each invaded animal are shown also a spherical contractile vacuole and an ellipsoidal nucleus. *C,* Sexual apparatus: *a–e,* five young zygosporangia, each resulting from the union of a mycelial hypha or hyphal branch with a germ tube from a conidium; *f–h,* mature zygosporangia, the relaxed membrane of each zygosporangium loosely surrounding the mature zygospore.

D–W, Acaulopage acanthospora: D, E, F, Portions of hypha, each of which has given rise to a bifurcate haustorium within a captured specimen of *Amoeba limax. G,* Portion of hypha that has given rise to a partly developed haustorium in a newly captured specimen of *A. limax, a;* and, close by, to a fully developed haustorium, which, on the nearly complete appropriation of the protoplasmic materials in the captured specimen of *A. limax, b,* has become partly evacuated. *H, I,* Portions of hypha, showing a more advanced stage in the withdrawal of contents from the haustorial branches in the largely depleted captured specimens of *A. limax. J,* Portion of a superficial hypha showing a captured specimen of *A. limax, a,* and a young growing conidium, *b. K,* Portion of hypha with a young conidium at a slightly later stage of development. *L,* Portion of mycelium with a fully grown but still immature conidium. *M–U,* Mature conidia in lateral view, showing variations in size, in shape, and in number and arrangement of the empty spiny appendages. *V, W,* Conidia in upper (*i.e.* distal polar) aspect.

STUDIES IN THE DEVELOPMENT OF TWO MYRIANGIUM SPECIES AND THE SYSTEMATIC POSITION OF THE ORDER MYRIANGIALES[1]

J. H. Miller

(WITH 4 FIGURES)

The peculiar characters of the ascocarp of *Myriangium* offer unusual possibilities for a phylogenetic study in the Ascomycetes. The well developed stroma and the septation of the spores have been considered derived, while the irregular positions of the asci in pseudoparenchyma, clavate to globose asci and no paraphyses, characterize plectomycete forms usually thought of as primitive. Also, in appearance the fruiting body is a typical apothecium, but the internal structure suggests the perithecium of the Plectascales. Interpretations of these characters have led to conflicting opinions, resulting in uncertainty in establishing the correct position for *Myriangium* and related forms in the Ascomycete system.

The two earliest described species, *Myriangium Duriaei* Mont. & Berk. and *M. Curtisii* Mont. & Berk., occur in abundance near Athens, and have therefore been the objects of this investigation. Emphasis has been placed on the origin of the ascocarp, and of the pseudoparenchyma separating the asci, and their initiation and development, and on a comparison of these characters with those found in orders of the Pyrenomycetes.

HISTORICAL REVIEW

The genus *Myriangium* was founded in 1845 by Montagne and Berkeley (**19**), with *M. Duriaei* as the type species. Later, they (**20**) added *M. Curtisii*, and placed both species in the lichen family, Collemaceae. The generic concept included a multilocular apothecium with asci in single locules.

[1] Contribution from the Department of Plant Pathology, University of Georgia.

In Die Natürlichen Pflanzenfamilien (**9**), 1897, the genus is in the family Myriangiaceae Nyl., and Fischer with the term " Anhang " doubtfully attaches it at the end of the order Plectascineae. He characterizes the family chiefly by the asci being embedded in the pseudoparenchyma of the fruiting body.

The order Myriangiales was erected by Starback (**25**) in 1899 to include a number of apparently related forms. The distinguishing characters of the order are an angiocarp fruiting body with asci arranged irregularly in a colorless plectenchyma and freed by the breaking away of the covering layer.

In 1917 Theissen and Sydow (**29**) enlarge the group still further, but retain the monascus locule as the chief character. Later, in 1918, they (**30**) propose the subclass " Dothidiineae " with three orders—1, Myriangiales, 2, Dothideales, and 3, Pseudosphaeriales. Again they relate them through the common basic character of the monascous locule. The Myriangiales are considered ancestral types from which have sprung the higher forms of the last two orders.

Gäumann and Dodge (**11**), in 1928, retain the order Myriangiales, but reduce the Pseudosphaeriales to family rank, and provisionally maintain the Dothideales. They describe the latter as Myriangiales with polyascous loculi.

Clements and Shear (**5**) place the Myriangiaceae in the Dothideales, because of the presence of stroma and locules.

Nannfeldt (**21**) in 1932 divides the Eu-ascomycetes into 1, Plectascales, 2, Ascoloculares, and 3, Ascohymeniales. The second group comprises those forms in which asci lie in locules, and includes the Myriangiales, Pseudosphaeriales, and Hemisphaeriales. The Ascohymeniales include all of those in which the asci and paraphyses form a genuine hymenium.

Recently Bessey (**2**) places the Myriangiales in the Pyrenomycetes, but says as the ascospores are many celled they should not be considered in a direct line of ancestry of the Pseudosphaeriales, Hemisphaeriales, or Sphaeriales.

The single character then according to Theissen and Sydow, Gäumann and Dodge and others that expresses relationship between forms they include in the Myriangiales, Pseudosphaeriales and Dothideales is the monascous locule. They would derive the

higher ones from the simpler Myriangiales by crowding and elongation of the asci and reduction of the stroma. This hypothesis would be correct only if the pseudoparenchyma separating the asci in *Myriangium* could be homologized with the interascal tissue of other forms now placed in the Myriangiales, or with the interthecial threads of the Pseudosphaeriales or Dothideales. However, this assumption has not been based on developmental studies, and it is not logical to determine relationships entirely from the picture presented by mature materials.

METHODS

These studies are based on paraffin sections from specimens gathered throughout the year, supplemented by living asci and ascospores. Attempts at cultures have been made, but without success in producing fruiting bodies. Several fixing solutions were used, but Fleming's strong was found most satisfactory for the later staining of nuclei with Haidenhain's iron-alum haematoxylin.

Thin serial sections, cut 2 to 3 microns in thickness, were necessary to distinguish details in the ascocarp, because of the unusual fineness of the stromatic elements.

MYRIANGIUM DURIAEI MONT. & BERK.

This species is well distributed over the world occurring as a parasite on scale insects on many kinds of trees. Seymour (24) lists eight species under six genera of the Coccidae as suscepts, and under host plants he gives *Carya illinoensis* (Wang) K. Koch, *Pyrus communis* L., *Crataegus* sp., *Citrus aurantium* L., *C. limetta* Riss., *C. limonia* Osb., and *Nyssa* sp. The writer finds *M. Duriaei* in Georgia chiefly on *Nyssa sylvatica* Marsh, and occasionally on *Nyssa biflora* Walt., *Carya illinoensis, Diospyros virginiana* L., and *Pyrus* spp.

The mature fructification consists of a black, fleshy to gelatinous, stroma with a flat base and indefinite form, 1.5 to 5 mm. in diameter, with one to many ascocarps. The latter in this species are discs, .5 to 1.5 mm. in diameter and .5 to 1 mm. high, usually constricted below. The surface is plane or convex with a distinct raised margin, but becomes concave following the discharge of the ascospores.

THE STROMA

Scales are found on both leaves and branches, but only those on the latter become infected, at least to the extent of developing a recognizable stroma. Dark mycelial mats form from the scale on the season's growth of wood, and during the summer these attain a diameter of 1 to 2 mm. They are then discrete, radially rugose, and slightly umbonate over the insect body.

The development of these mats progresses from loosely interwoven dark hyphae found in the insect. As they emerge from the shell they coalesce forming a compact stromatic body of parallel thick-walled hyphae. From this point on the growing region is confined to the peripheral cells. The latter divide rapidly in several planes cutting off uninucleate cells of dense protoplasm. As the stroma advances in age the sections (FIG. 4:1) show very small sclerotid cells forming a pseudoparenchymatous tissue.

Sections through the young stroma show some penetration into lenticels, producing a very close attachment to the young bark, and cells directly under the center soon die.

In early summer the fungus goes into a resting stage, resuming growth after the usual dry season in Georgia. Afterwards, when rains begin in the late summer or early fall, live parts divide rapidly increasing the stromal diameter, and then the ascocarps arise. The latter are in process of development during the fall and winter, and the ascospores mature in late winter or early spring.

After ascospore expulsion either all of the stroma or much of it dies, but live parts will produce ascocarps again the next year. In this manner there is perennial growth for several years, or at least until the branch dies. No live stromata have been found on dead limbs. The youngest stromata are then on the season's growth, and progressively older ones are found on the older branches. This can be accounted for by the presence of scales chiefly on the young bark.

Reproduction is entirely by ascospores. No evidence of conidial formation was found on stromata of any age nor in cultures.

THE ASCOCARP

1. The archicarp: After the resting period coils arise just under the periphery of the central thicker portions (FIG. 4: 1, 2). This takes place in August and September in Georgia. All coils have been found only in the beginning of renewed growth, and never in continuous growth from the stromatic initials. The surrounding cells receive sufficient growth stimulus to form a slight protuberance. The archicarp (FIG. 1: 1–*a*) consists of a coiled, vertically elongated, septate hypha with attenuated upper cells, the trichogyne. The one to three much enlarged middle or lower cells constitute the ascogonial region. The stalk and trichogyne cells are chiefly uninucleate, while the enlarged ones contain many nuclei, some of which are in pairs.

Near the archicarp there is usually another hypha (FIG. 1: 1–*b*) of approximately the same length entering into a loose coil. This thread is multicellular, and each cell contains one or two nuclei. It has the position and appearance of an antheridium, but no sections were found showing actual fusion of tip cells. The chief evidence against a fusion lies in the presence of nuclei in this hypha when paired nuclei are to be seen in the ascogonial cells. This suggests apogamy, but it is not logical to conclude such to be the case until more evidence is produced.

There is no possibility of fertilization from spermatia, as none were found either on the surface of the stroma or within fructifications.

2. Ascogonia: The primary ascogonial cell divides repeatedly cutting off a layer of deeply staining enlarged multinucleate cells (FIG. 1: 2–*a*, 3–*a*). Lateral divisions result in an expansion of the ascocarp, while divisions forming cross walls initiate the ascogenous hyphae. A longitudinal section of *M. Duriaei* (FIG. 4: 3, 4) at this point shows a concave layer of secondary ascogonia forming the base of the disc. This layer definitely separates the fertile region from the underlying stroma.

3. Ascogenous hyphae: Two nuclei are cut off in the terminal cell of each ascogonium. These binucleate cells continue dividing, ultimately forming a system of vertical chains. These are the ascogenous hyphae (FIG. 1: 4). At the stage shown in figure 4:

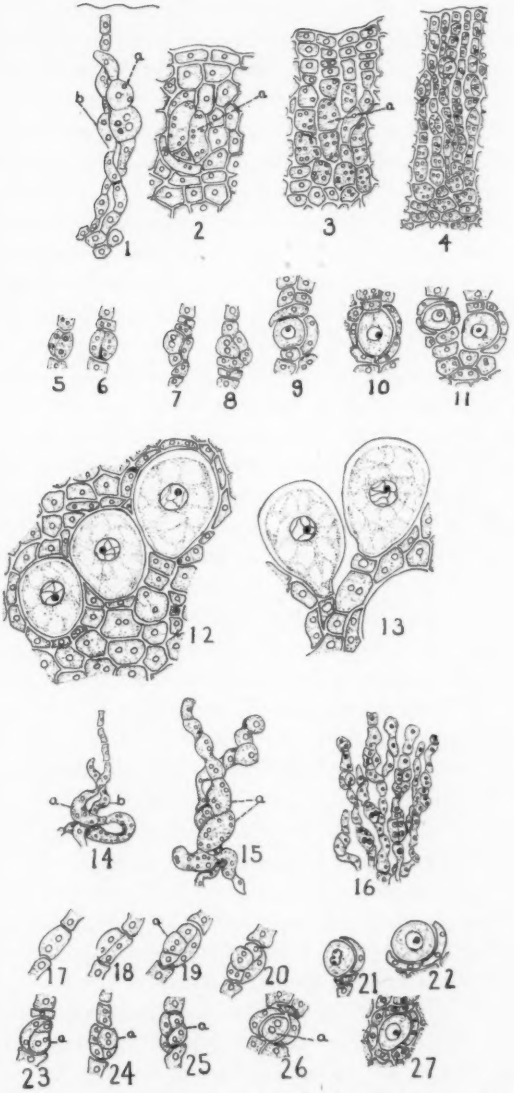

FIG. 1. 1–13, *Myriangium Duriaei*; 14–27, *Myriangium Curtisii*.

3, 4 the entire tissue of the disc consists of these hyphae. Also, in *M. Duriaei* all of this system arises from one coil.

The concavity of the disc is due to the oldest ascogonia, and so oldest and therefore longest vertical chains of ascogenous hyphae, being in the center. Longitudinal divisions in intercalary or terminal cells, resulting in many secondary branches, along with ascal growth, account for the lateral expansion.

In this growing system of primary ascogenous hyphae all cells are binucleate with an occasional one containing three or even four nuclei. However, in further divisions these nuclei do not always divide conjugately, and so in a mature system component cells contain either one or two.

No evidence of hook formation was found, and all branches come from longitudinal or diagonal divisions.

4. Formation of asci: This begins in late September and continues on throughout the fall. Binucleate cells in the ascogenous hyphae, either terminal or intercalary, divide longitudinally or diagonally to form an ascus. One of the binucleate daughters (FIG. 1:5) then enlarges laterally, and the two nuclei divide again, with separate spindles, putting down two cross walls. The latter cut off two nuclei of apparently opposite sex in the central cell (FIG. 1:6). This cell now greatly enlarges to form the ascus. At this early stage the young globose ascus (FIG. 1:7,8) is surrounded by several much curved, very thin cells. These are the back cell and the upper and lower cells of the first divisions. Their shape is due to the pressure of the developing ascus. In some cases the lower cell (FIG. 1:13), formed from the second division, appears as a stalk to the ascus, but usually the latter is a direct outgrowth without even the appearance of a stalk.

The remaining cells in the ascal complex often continue to divide. When this is in an intercalary cell of the hypha many small cells or branches arise, but when in a terminal cell the upper or back cell will continue the ascogenous hypha upward.

Asci form all along the length of the hypha with the exception of the extremities. The regions then just above the ascogonia and just under the surface (FIG. 4:5) do not contain asci.

The development of asci is more or less simultaneous in any one hypha, but marginal hyphae, being the last formed, contain the

youngest. In a section approaching maturity (FIG. 4:5) the oldest asci are in the center, decreasing in age towards the margin.

The only similarity between the origin of asci in *Myriangium* and the crozier formation as described by Harper (**14**), Claussen (**4**), and others lies in two simultaneous divisions resulting in two nuclei of supposedly opposite sex being cut off in one cell that will become the ascus. The difference is that in these fungi neither the apical nor intercalary cells proliferate to form the characteristic hook. Also, this development results in the asci being interspersed among the ascogenous hyphae, and not in a layer above them as in *Pyronema confluens,* and many other Discomycetes and Pyrenomycetes.

5. Divisions in the ascus: The two nuclei (FIG. 1:8) in the ascus fuse directly after the latter is cut off and still very small. This occurs during the early fall in Georgia. Following this the nucleoli remain distinct for several weeks and then fuse. The fusion nucleus (FIG. 1:9, 10, 11 and FIG. 3:1) enlarges to at least twice the size of the originals, and stains uniformly. Then it enters a resting period of from one to three months. Divisions begin in late December or early January.

Just before dividing (FIG. 2:2 and FIG. 3:2) there is further expansion, and the chromatin material appears as dark, deeply staining, lines that make several loops. Other nuclear materials do not stain now, and as one focuses up and down, the spireme seems to be in a clear field. Later, the thread thickens (FIG. 2:3, 4), and four double, slightly elongated, masses can be distinguished. These chromosomes are very small and details are determined with difficulty, but this is evidently synapsis. In the later stages of synapsis they appear as very small black dots. Next the nuclear wall disappears, and a spindle forms in the center, or to one side of an elongated clear space. Four chromosomes (FIG. 2:5) pass to each pole. After the separation the two daughter nuclei are organized. A second division and a third (FIG. 2:7, 8, 9) follow immediately, and eight daughter nuclei, each in the center of a clear field, occupy the ascus. Each contains four chromosomes, and so the last two divisions are probably equational, and the reduction is accomplished in the first.

6. Formation of ascospores: Immediately following the third

division in the ascus the eight chromatin masses reconstruct nuclear membranes. These are at first cone shaped. The apex of the cone gradually elongates forming something like a distended neck of a bottle. At this stage the nuclear beaks (FIG. 2: 12) become oriented toward the apex of the ascus. The spore walls are now delimited along lines of the astral rays as described by

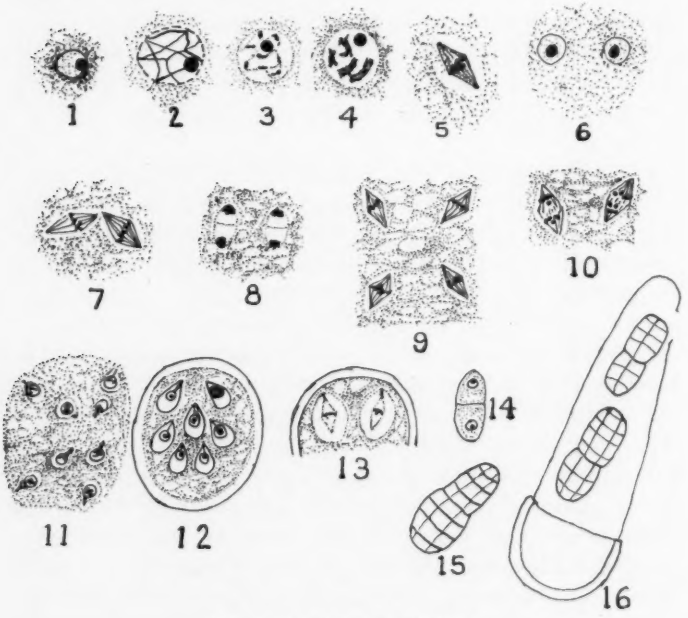

FIG. 2. *Myriangium Duriaei.*

Harper (**13**). The young spore at this stage, with the exception of the nucleus and beak, does not stain, and appears hyaline in contrast to the deeply staining epiplasm.

When the beak disappears and the spore rounds out at the apex the nucleus divides again (FIG. 2: 13). A plate forms at this time, and an elliptical spore (FIG. 2: 14), slightly constricted at the cross wall, is formed. Immediately the two nuclei continue dividing rapidly, ultimately forming a muriform spore with five to seven cross walls, and one to four longitudinal ones. The mature spore (FIG. 2: 15) is light greenish-yellow and 12–14 × 25–36 μ.

7. Eruption of the ascus and expulsion of the ascospores: The spores mature in Georgia in March and April. During the first warm, wet weather the fertile portion absorbs much water and is then soft and gelatinous. The asci swell greatly, and each pushes through the surface independently. There is no covering layer of the ascocarp that sloughs off. Those nearest the surface break through first. Looking down at a mature fruiting body the glistening rounded tips of the asci can be seen throughout the surface. The thick ascal wall now separates into an outer, rather thick one, and an inner thin layer. In dehiscence the outer one splits transversely and collapses, and the inner (FIG. 2: 16) expands upward beyond the surface of the ascocarp. The enlarged ascus is now two or three times the length of the original. The break may occur near the apex or in the side of the ascus, and the spores are expelled several inches from the fruiting body.

The lower asci push up through the cavities left by the disappearance of the upper ones and repeat the process. In this manner the entire fruiting body will discharge its ascospores in one to two weeks, and then it becomes quite concave with the subsequent shrinkage.

8. Germination of the ascospores: The spores germinate freely in distilled water on a slide. Every cell puts out a germ tube, and at room temperatures a mycelial mat of close hyphae will form within twenty-four hours. In nutrient agar there is more rapid growth and germ tubes of smaller diameter.

MYRIANGIUM CURTISII MONT. & BERK.

Judging from the literature this species is confined to the Southern States. It also occurs as a parasite on members of the Coccidae on various trees. Seymour (**24**) lists it on *Carya illinoensis, Citrus aurantium, Gleditsia triacanthos* L., and *Crataegus mollis* (T. & G.) Sch. Miles (**16**) describes the fungus on pecan under the name *M. tuberculans*. In Georgia the writer finds it on *Crataegus aprica* Beadl. and *C. uniflora* Moench. Other *Crataegus* species, such as *C. spathulata* Michx. and *C. cordata* Ait., even when in a clump with the above are not affected.

THE STROMA

Hyphae emerge from the body of a parasitized scale. These grow radially, coalescing to form a flat rugose stroma very much like the early stages of *M. Duriaei*. From this point on there is much more upright growth than in the latter, so the mature fructification is from .5 to 2 mm. thick. The sterile context is a light lemon yellow in color, and remains alive from one to two years. The dead parts are reddish-brown as in the other species. This stroma is composed of interwoven prosenchymatous threads of thick walls and fine lumen, and there is not the small compact pseudoparenchyma of *M. Duriaei*.

THE ASCOCARP

The fruiting bodies on the mature stroma are flat to convex, circular or irregular due to mutual pressure, and are completely sessile. There is no constriction under the fertile region. From 30 to 50 ascocarps form on the surface of the hemispheric stroma.

The most striking difference between this species and *M. Duriaei* lies in the shape of the fruiting bodies. In the former (FIG. 4:7) the section shows a figure with the border and lower line parallel, while the latter (FIG. 4:5) is a triangle. The shape along with the context differences are sufficient grounds for maintaining two species.

1. The archicarp: As in *Myriangium Duriaei* it arises in renewed growth from the resting stroma in late summer, and is not found in continuous growth from the initial stroma. Flat layers of hyaline hyphae growing from peripheral convolutions form a layer concentric to the curvature of the stroma. This fertile layer of *M. Curtisii* arises from many separate archicarps instead of only one as in *M. Duriaei*.

The archicarps are embedded in the fertile region as in the other species. The hypha (FIG. 1:14) is elongated upward, loosely coiled with one or more very large lower cells. A possible antheridium is seen in the coil. The tip cells do not penetrate the surface. Also, no fusion of tips was observed in this species. No spermatea nor even conidia were found.

2. Ascogonia: The basal cells divide in longitudinal and cross planes cutting off a few very large cells with many nuclei (FIG.

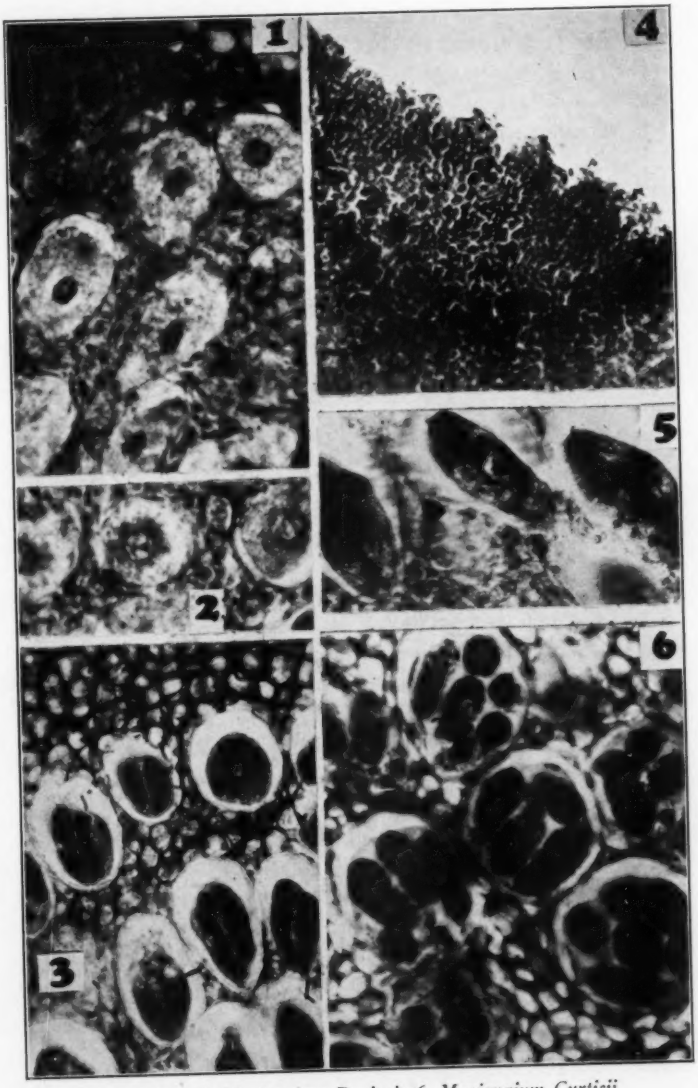

FIG. 3. 1–5, *Myriangium Duriaei*; 6, *Myriangium Curtisii*.

1:15). Some of the latter were found in pairs. These do not repeat the process to form a continuous basal layer of ascogonia as in *M. Duriaei*. In the base of the fertile region in *M. Curtisii* then there are many separate patches of ascogonia.

3. Ascogenous hyphae: These are formed by cross divisions in the upper part of each ascogonium cutting off binucleate cells. Later divisions produce chains of hyphae (FIG. 1:16), which develop upward in the shape of a fan. At this stage the entire ascocarp is penetrated by overlapping systems of these hyphae, and while they compose most of the tissue, some of it is made up of the original vegetative cells. This is in sharp contrast to the structure of *M. Duriaei* in which the fertile part is entirely ascogenous hyphae and asci. The disc in *M. Curtisii* then is a compound structure.

The formation of asci, the nuclear divisions in the ascus, as well as ascospore formation proceed as in *M. Duriaei*. It is impossible to distinguish the mature ascospores from those of the other species.

Myriangium Curtisii bears a very close morphological resemblance to *M. Bambusae* Rick. The latter is the only other member of the group that has been the subject of a developmental investigation. Tai (**27**) describes a sterile stroma and a delimited fertile region. The asci arise from fertile filaments that proceed from enlarged basal cells. They are spherical and double walled, and dehiscence is as in the ones described above. His interpretation of the origin of the ascus, however, is entirely different from that of the writer. He says the ascus arises from the enlarged end cell of a coil, and then basal parts of the coil grow around this enlarged cell in one or two layers, and the latter finally disintegrate to form an outer wall or sheath to the mature ascus. No evidence of such a coil was found in either *M. Duriaei* or *M. Curtisii*, and the surrounding cells are all parts of adjoining ascogenous hyphae, and their shape is due to the pressure of the enlarging ascus. Also, the thick ascus wall is homogeneous from the first, and no breakdown of nearby cells was observed.

The double wall and the subsequent splitting has been interpreted variedly in *Myriangium* and related genera. Miles (**16**) with *M. Curtisii* describes a thick hyaline sheath which surrounds

the wall of the ascus. Stevens and Weedon (**26**) think when the wall ruptures the surface of the expanding ascus is only epiplasm simulating a wall. Millardet (**17**), in his historical figures, shows an ascus expanding from an outer sheath. Petch (**22**) finds the same action in *M. Duriaei.* Also, Jenkins (**15**) describes it for a related form, *Elsinoe Canavaliae.*

AFFINITIES OF THE FORMS NOW PLACED IN THE MYRIANGIALES

In the Synoptische Tafeln, Theissen and Sydow (**29**) characterize the order by a stromatic angiocarp fruiting body with asci in one or several layers, but all forms have the asci in single locules. The six families and many genera and species they describe under this order should have the fundamental characters of *M. Duriaei,* the type of the group.

The Myriangiales concept then should consist of a stromatic form in which the archicarp gives rise to a layer of ascogonia from which develops the upright branching system of ascogenous hyphae. Globose asci are formed from lateral and terminal expansions of cells within the hypha, and therefore appear many layered in the fertile portion. Each ascus is separated by cells of adjoining ascogenous hyphae. The elliptical, divided, ascospores are ejected by the elongation of the inner wall of the ascus pushing through the surface and forcibly expelling the spores.

Theissen and Sydow describe the Elsinoëae v. Höh., Plectodiscelleae Wor., Myxomyriangiaceae Th., and the Myriangiaceae Nyl. within the above concept. The species have several layered asci, which means ascogenous hyphae as interthecial tissue, and spherical asci with elliptical, divided spores. The separations are based on whether the fruiting body is delimited from the sterile stroma, and characters of the covering layer.

The other families they include in the order, the Saccardiaceae v. Hoh. and Dothioraceae Theiss. & Syd., have the asci in a single layer. The writer has not been able to make a critical study of any member of the former family, but the single layer of asci shows that the locules are stromatic, and so are not the same as the locules in the Myriangiaceae. However, their affinities cannot be accurately determined until ontogenetic studies have been made of some of the species.

The Dothioraceae is separated from the Saccardiaceae by having the interthecial stroma separating the asci paraphyses-like instead of cellular, and asci elongate, close and parallel.

Later, Theissen and Sydow (**30**) erect the order Pseudosphaeriales, and place in it some of the genera previously in the Dothioraceae, and some that were in the Dothideales and Sphaeriales. The ordinal characters include small perithecium-like forms with asci in a single layer, and separated by thread-like strands. This group includes such forms as the species of *Leptosphaeria, Pleospora, Botryosphaeria, Dibotryon, Apiosporina, Cucurbitaria* and others.

Gäumann and Dodge (**11**) maintain the Dothioraceae and Pseudosphaeriaceae as separate families and make them the advanced points in the Myriangiales. The family distinctions are based on the number of ascal groups found in the stroma. The compound form, as *Botryosphaeria*, would be in the Dothioraceae, and the simple one, as *Physalospora*, would be placed in the Pseudosphaeriaceae. The latter, according to them, would be transitions to the simple perithecia of the Sphaeriales.

Before one can determine whether there is a relationship between the Pseudosphaeriales, or other Pyrenomycetes and the Myriangiales, the character of the interascal tissue must be recognized. This is more fundamental than the shape or size of the fruiting body. The writer (**18**) has previously found two principal types of ascocarps in the Pyrenomycetes.

1. True perithecia with walls that arise from the basal cells of the archicarp, the upper wall cells proliferating upward to form a definite ostiole, asci forming a wall layer, interspersed with true paraphyses (sterile threads with free ends), and periphyses in the ostiolar canal. This type is common to members of the Sphaeriales and Hypocreales orders. There is no semblance of monascal locule, and so this type has not been connected with *Myriangium* by any of the above writers. The group would be included in the Ascohymeniales of Nannfeldt (**21**).

2. The ascocarp has no true ostiole, opening by a break in the wall above the asci, and there are no paraphyses. This is the dothideaceous stroma of the above paper, and the Ascoloculares

in part of Nannfeldt. Since then the writer has found two subdivisions of this group.

a. Ascocarp single or compound, asci from short ascogenous hyphae, forming a fascicle, and growing upward in more or less pseudoparenchymatous tissue. This is seen in single forms in members of the Mycosphaerellaceae, and in compound ones in *Dothidea* species.

b. Ascocarp single or compound, asci forming a concave layer as in a true perithecium, sterile threads connected at the top and bottom of the cavity with the asci growing upward between them. These are the "paraphasoiden" found in species of *Pleospora, Boytrosphaeria, Cucurbitaria, Dibotryon* and others of the families Dothioraceae or Pseudosphaeriaceae.

The genera in keys to the Dothideales by Clements and Shear (**5**), or Theissen and Sydow (**28**), separated by "paraphyses none," belong to type "*a*." In *Dothidea* or *Mycosphaerella* species there are non-motile sperms, fasciculate asci, and interthecial tissue of stromal remnants, and so the structures in this type cannot be homologized with analogous ones in *Myriangium*.

In group "*b*" the interthecial threads appear in the position of the future cavity before the asci arise. Also, these threads develop from a coiled archicarp. The asci arise in their bases, and in maturing grow upward among them. The slenderness of the threads then is not due to the compression or digestion of the developing asci as thought by Theissen and Sydow, Gäumann and Dodge, and others.

The function of the "paraphysoiden" has been variously interpreted. Cavara and Mollica (**3**) in their figures 41–45 on the development of *Pleospora herbarum*, depict asci arising in the cells of parallel hyphae.

Sartoris and Kauffman (**23**) describe the asci as being formed as basal cells of the threads in *Apiosporina Collinsii*. The upper part of the thread breaks off of the developing asci, and the latter continue upward among hyphae attached only above.

Arnold (**1**), with *Sporormia leporina*, says, "As the perithecium grows and the vertical hyphae become more numerous the enlarged cells at their tips form a rather definite zone across the lower part of the cavity. . . . It is from these enlarged cells at

the tips of the vertical hyphae that the ascogenous hyphae appear to arise. They elongate upward, *i.e.* in the opposite direction from that of the vertical hyphae."

According to these authors the vertical threads would appear to be ascogenous hyphae. This is again fundamentally different from the locule in *Myriangium* where the ascogenous hyphae grow upward, rather than downward, and the asci arise laterally.

All three types of centra described above, along with those of the Myriangiales, are to be found in the Dothideales as erected by Clements and Shear (**5**). In the Dothideae those "without paraphyses" include type "*2–a*," and "paraphyses present" are "*2–b*," and *Phyllachora* in the same family is found with true paraphyses as in type "1." Also, in the Myriangiaceae they include some genera with asci separated by paraphyses-like threads, or "Paraphysoiden." Then they remove *Botryosphaeria*, a genus of type "*2–b*," from its position in the Sphaeriales to the Dothideales, but leave *Physalospora*, a closely related genus, in the former order. The chief difference between the two consists in the degree of stroma.

The characters exhibited by the ascigerous centrum appear to be of more fundamental importance in indicating relationship, than the size of the fruiting body, or the amount of stroma. So fungi with true paraphyses should remain as the basis of the Sphaeriales; those with no threads, as in type "*2–a*" should comprise the Dothideales, and those with paraphyses-like threads, should make up the Pseudosphaeriales. Then this last type "*2–b*," now found in the Dothioraceae and Pseudosphaeriaceae in the Myriangiales, according to Gäumann and Dodge (**11**), should be placed in the Pseudosphaeriales.

RELATIONSHIP OF THE MYRIANGIALES TO THE PLECTOMYCETES

There is some uncertainty of opinion among mycologist as evidenced by most modern ones placing the Myriangiales with the higher Pyrenomycetes, but still recognizing their plectomycete affinities. The usually accepted separation of the last two groups is that given by Schroter (**9**) in which the Plectascineae have asci at different levels, and the Pyrenomycetineae have them in tufts or fascicles. The most distinctive point is the manner in which the

asci are borne. In nearly all of the Plectomycetes the asci are borne either terminally or laterally from proliferating ascogenous hyphae, which arranges them at irregular levels throughout the fertile region, while in the Pyrenomycetes they are usually formed from the penultimate cell of a hook and are left in a fascicle or straight layer.

Gäumann and Dodge (**11**) distinguish the Plectascales by the possession of "angiocarpous perithecia without ostioles, whose whole interior is irregularly penetrated by ascogenous hyphae, consequently the asci (generally spherical) lie scattered irregularly in the ground tissue of the fructification." The Plectomycetes are considered in the Pyrenomycetes, but they place the Plectascales, Perisporiales and Myriangiales in one group with ascospores liberated only on decay of the perithecia, and in the other group are found perithecia which have regular openings.

Clements and Shear (**5**) place the simpler Plectomycetes in the Gymnoascales, the forms with perithecia in the Perisporiales, and the tuber-like ones in the Tuberales. *Aspergillus* and *Penicillium*, with perithecium-like ascomata, but with asci at irregular levels, are found in the same order with the Erysiphaceae having asci in single fascicles. Also, they aline the Myriangiaceae in the Dothideales order on the basis of the locules, but recognize the plectomycete nature by stating that, "The Gymnoascaceae lead directly into the Eurotiaceae on the one hand and the Myriangiaceae on the other; no real dividing line being discernible in the latter case especially."

Gwynne-Vaughan and Barnes (**12**) separate the Plectomycetes from the Discomycetes and Pyrenomycetes by "ascocarp, if present, either with no definite ostiole, or shield-shaped, or with asci irregularly arranged." The Plectascales are delimited by the last part of the definition.

The series in the Plectascales, according to the above authors, begins with naked asci, and no ascogenous hyphae, and continues to ones completely inclosed in a well defined peridium with a much branched hymenium, no paraphyses, globose to pyriform asci, and no regular method for the ascocarp to open.

Bessey (**2**) in describing the Plectascales says the ascogenous hyphae are of varying lengths, so that instead of arising in a tuft the asci are produced throughout the interior of the perithecium.

Previous investigations in the Aspergillaceae show them to possess many characters in common with *M. Duriaei.* Fraser and Chambers (**10**), with *Aspergillus herbariorum,* found an archicarp consisting of a stalk, a unicellular ascogonium, and a unicellular trichogyne. The ascogonium divides into a number of multinucleate cells, each of which buds out ascogenous hyphae.

Dale (**6**), with *Aspergillus repens,* describes a coiled archicarp, and this may have any number of septa; so it is impossible to distinguish trichogyne, ascogonium, and stalk, and in some cases ascogenous hyphae arise along the whole length of the coil. The female branch in *M. Duriaei* consists of similar parts, and differs in development only in many secondary ascogonia arising from the first multinucleate cell. Also, in *Aspergillus repens,* as in all members of the Plectascales investigated, the sex branches consist of antheridium and archicarp just as in *M. Duriaei,* while in the higher Pyrenomycetes non-motile sperms are the rule.

The ascus in *Myriangium* arises from outgrowths of cells along the entire length of the ascogenous hyphae with the exception of the indeterminate apex, while in the *Aspergillus* species of the above author they arise from either the penultimate cell or from the terminal. Dodge (**8**) with *Penicillium Brefeldianum* says, "The ascus usually arises as a side or terminal bud from a cell of an ascogenous branch." His figure 2, *d* shows asci laterally placed on septate hyphae arising from one side of a curved branch, which is very much like the condition in *Myriangium.*

While ascus formation is typically without the crozier in the Plectascales, De Lamater (**7**) finds an exception in *Arachniotus aureus* (Eid.) Schr. The coiling female cell begins to be cut up into binucleate cells which are usually very nearly isodiametric. The ascus arises from typical hooks from each binucleate cell of the female branch.

The mature ascocarp contains asci scattered irregularly in between branches of ascogenous hyphae in *Myriangium* and in the perithecia of the Aspergillaceae of the above authors. However, in the latter family there is not the stromatic development of *Myriangium,* and the perithecia are very small and definite in shape in contrast to the almost discomycete cupules found on the stroma. The nearest approach in stromatic pseudoparenchyma is found in some species of *Penicillium.*

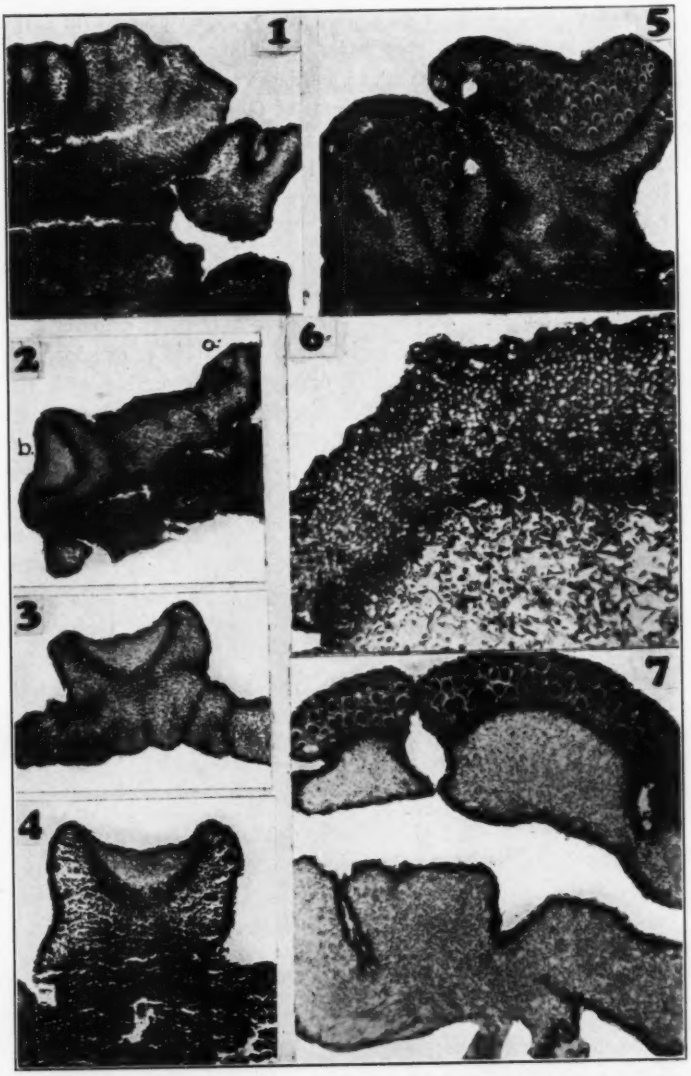

FIG. 4. 1–5, *Myriangium Duriaei;* 6–7, *Myriangium Curtisii.*

Among the higher Plectascales the Onygenaceae form large fruiting bodies with sterile bases, but their affinities with *Myriangium* cannot be determined until developmental studies have been made. The writer has sections of *Onygena equina*, and these show a fertile capitate region on a pseudoparenchymatous stalk. The asci are arranged at irregular levels throughout the head, but the ground tissue is more prosenchymatous, and is not made of the coalesced hyphae of *Myriangium*. So while *Myriangium* shows some striking similarities to *Onygena*, it is probable that the latter is in a direct line of the more fleshy forms leading through Elaphomyces to the Tuberales, and *Myriangium* may be on another line.

The families of the Myriangiales show progressive development in stroma and definiteness of fruiting body beginning with the Elsinoëae, through the Plectodiscelleae, the Myxomyriangiaceae, and finally the Myriangiaceae. In *Elsinoe* species the stroma consists of an undifferentiated colorless plectenchyma with asci irregularly placed, which is not very far from *Gymnoascus* or *Ctenomyces*. The Myriangiales, then, probably arose through *Elsinoe* from an ancester at the Gymnoascaceae level, and form a separate branch ending with the disc-like ascocarps of *Myriangium* species. In a natural system they should be placed next to the Plectascales, and the present tendency to aline them with the Pyrenomycetes (Pseudosphaeriales, Dothideales, Hypocreales and Sphaeriales) is untenable, as none of them produce perithecia, nor have the internal arrangement of members of these orders.

SUMMARY

The characters of *Myriangium Duriaei* and *M. Curtisii* have been studied in serial sections. The fertile disc in the former arises from one archicarp, and consists of asci and ascogenous hyphae; while in the latter the disc is compound, consisting of several such systems.

The ascal locule cannot be homologized with the locule in the Pseudosphaeriales nor in the Dothideales, because the interthecial tissue is ontogenetically different in each case. So these orders cannot have their roots in the Myriangiales through the monascous locule.

The globose asci, arising from lateral or terminal positions on

the ascogenous hyphae, and being separated by these hyphae at different levels, are all characters which indicate a close Plectascales relationship.

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EXPLANATION OF FIGURES

FIG. 1. *Myriangium Duriaei:* 1–13, drawn with the aid of the camera lucida at the same magnification. 1. Sex branches, *a*, archicarp, *b*, antheridium. 2. Secondary ascogonia at *a*. 3. Further division beginning the layer of secondary ascogonia, and the chains of small cells constituting the ascogenous hyphae. 4. Chains of ascogenous hyphae forming the fertile region. 5. Longitudinal division of an intercalary cell, the first step in ascus formation. 6. Two divisions in one of the daughter cells, cutting off two nuclei of opposite sex in the central cell. 7–8. Enlargement of this cell to form the ascus and beginning of nuclear fusion. 9. Growing ascus with enlarged fused nucleus. 10–11. Further divisions of remaining cells in the ascal complex. 12–13. Asci after the resting period, showing the enlarged nuclei with spiremes.

Myriangium Curtisii: 14–27, drawn as the above species. 14. Sex branches, *a*, archicarp, *b*, antheridium. 15. Further divisions showing several enlarged ascogonial cells. 16. Fan-shaped group of ascogenous hyphae. 17. A binucleate cell in an ascogenous hypha. 18. First longitudinal division in ascus formation. 19. Divisions in a daughter cell with the young ascus at *a*. 20. Rounding out of ascus. 21. Fusion of nuclei. 22. Enlarged ascus with nucleus going into a resting stage. 23–26–*a*. Various views of young ascus, each depending on the manner in which the section is cut. 27. Enlarged ascus showing the compression of the surrounding cells. Magnification of above drawings: × 560.

FIG. 2. *Myriangium Duriaei.* Drawn with camera lucida. 1. Fusion nucleus in resting stage in ascus. 2. Nucleus much enlarged showing spireme loops. 3. Spireme breaking up into chromosomes. 4. Showing four double chromosomes in synapsis. 5. The nuclear wall has disappeared and

the four synaptic pairs are seen on the equator. 6. End of the first division in the ascus with the reorganization of the two daughter nuclei. 7. Late metaphase in the second division. 8. A telophase of this division. 9. Metaphase of the third division. 10. Anaphase with four chromosomes passing to each pole. 11. Reorganization of the eight nuclei in the ascus. 12. Each nucleus, with a beak from the centrosome, becomes oriented towards the apex of the ascus. 13. Metaphase of the first division in the young ascospore. 14. Young ascospore with cross wall. 15. Mature spore. 16. Mature ascus erupting. The outer thick wall is shown collapsed at the base, and the inner wall expands vertically. 1–11 × 1250. 12–13 × 950. 14–16 × 850.

FIG. 3. Photomicrographs of ascospore formation. 1–5. *Myriangium Duriaei*. 1. Resting nucleus in October. 2. The fusion nucleus is beginning the reduction division. The nucleolus and spireme loups appear in a clear field. 3. Immature ascospores. 4. Section of ascocarp showing the layer of large ascogonial cells at the base and ascogenous hyphae with very young asci. 5. Anaphase of first division in the spore before it is entirely delimited. 6. *Myriangium Curtisii*—mature ascospores. 1, 2, 3, 5, 6, × 850. 4, × 270.

FIG. 4. Photomicrographs of longitudinal sections of ascocarps. 1–5. *Myriangium Duriaei*. 1. Coils develop in the indentations in the apices of the stromatic protuberances. 2–*a*. Coil beginning development. *b*. More advanced fertile region entirely filled with ascogenous hyphae. 3–4. These show the concave basal layer of ascogonia separating the fertile portion from the stroma. 5. Ascocarp about mature. × 58.

6–7. *Myriangium Curtisii*. 6. Section through fertile region showing parts of archicarps in the darkened areas. 7. A mature ascocarp. 6, × 270. 7, × 58.

THE EFFECT OF TEMPERATURE ON ASCI AND ASCOSPORES IN THE GENUS DEBARYOMYCES

E. M. Mrak and Lee Bonar

(with 2 figures)

An important character used for the differentiation of the genus *Debaryomyces* is the presence of warty irregularities on the ascospore walls. Guilliermond ('28) and Stelling-Dekker ('31) pointed out that it is sometimes difficult to observe these irregularities. Ota ('24) found that the ascospores of old cultures of *D. Fabryi* were not warty. The writers have observed that the ease with which these warty irregularities can be seen varies in different cultures of the same organism. Casual observation indicated that the ascospores from cultures, grown in an unheated room in winter, were more distinct than those grown in the same room in summer.

The room temperature at which different cultures of the same organisms were grown varied considerably with the season of the year. There is no available information, as far as can be determined, concerning the effect of temperature on the appearance of asci and ascospores of the genus *Debaryomyces*.

A series of tests have been conducted to determine the effect of temperature on the morphology of ascospores and asci produced at various temperatures on Garodkowa agar slants. Ten film forming cultures of *Debaryomyces*[1] found in California and cultures of *D. Guilliermondii* Dekker, *D. Guilliermondii* var. *new zealandicus* Lodder, *D. membraneafaciens* Naganishi, and *D. membraneafaciens* var. *hollandicus* Lodder, obtained from the "Centraalbureau voor Schimmelcultures," were used in this study. Garodkowa agar slants were inoculated from active liquid wort cultures and duplicate tubes of each organism were incubated at 7, 10, 16, 22, and 28° C. Cultures of *D. Guilliermondii* var. *new*

[1] The taxonomy of these organisms will be discussed in a subsequent paper.

zealandicus and *D. membraneafaciens* were also stored at 4° C. and cultures of the 4 organisms obtained from the "C. B. S." were incubated at room temperature. The cultures were examined frequently for spore formation. Measurements were made, with an eye piece micrometer, of 25 ascospores and their respective asci and 25 vegetative cells when spores were first observed. An example of the typical data obtained for the 14 cultures is given in table I.

TABLE I

DIMENSIONS IN MICRONS OF ASCOSPORES, ASCI AND VEGETATIVE CELLS FROM CULTURES OF *D. Guilliermondii* VAR. *new zealandicus* LODDER SHOWING THE TYPE OF VARIATION OBSERVED IN THE 14 CULTURES STUDIED

Incubation Temperature Centigrade	Spore		Ascus		Vegetative Cells	
	Average	Extremes	Average	Extremes	Average	Extremes
4	3.2 ×3.2	2.9–3.4× 2.9–3.4	5.6×6.3	4.6–6.9× 5.2–6.9	5.3 ×5.45	4.0–6.3× 4.0–6.9
7	3.25×3.25	2.3–3.4× 2.3–3.4	4.5×4.95	3.4–5.3× 3.4–6.3	3.8 ×4.0	2.9–5.2× 2.9–5.8
10	3.3 ×3.3	2.9–3.7× 2.9–3.7	4.2×4.5	3.4–4.6× 3.4–5.3	4.3 ×4.3	2.9–5.3× 2.9–5.3
16	3.0 ×3.0	2.9–3.4× 2.9–3.4	3.9×4.2	3.4–4.6× 3.4–5.3	4.25×4.25	3.4–5.2× 3.4–5.2
22	3.3 ×3.3	2.6–3.7× 2.6–3.7	3.8×3.9	2.9–4.6× 2.9–4.6	4.2 ×4.2	3.4–5.2× 3.4–5.2
25	3.3 ×3.3	2.9–4.0× 2.9–4.0	3.9×4.0	3.4–4.6× 3.4–4.6	4.0 ×4.1	2.9–4.9× 2.9–4.9
28	3.4 ×3.4	2.9–3.7× 2.9–3.7	4.0×4.3	3.4–4.6× 3.4–4.6	3.85×3.85	2.9–5.3× 2.9–5.3
Room	3.2 ×3.2	2.9–4.0× 2.9–4.0	4.0×4.1	3.4–4.6× 3.4–4.6	3.9 ×3.9	2.9–5.2× 2.9–5.2

In nearly all instances ascospores produced at temperatures below 22° C. were more easily observed than those produced at 22° C. or above. Irregularities were present on the walls of the ascospores of all cultures observed but were more easily seen when the cultures were incubated at the lower temperatures. In many instances when cultures were incubated above 22° C. it was very difficult to differentiate the ascospore and ascus. In these instances

the organisms had the appearance of spherical cells with a dense layer of protoplasm surrounding a large vacuole. Such a condition could easily lead to the inclusion of certain members of the genus *Debaryomyces* in the imperfect film forming yeasts. When the asci were only slightly larger than the ascospores it was necessary to stain the cells with Loeffler's methylene blue diluted 1–100 in order to distinguish the spores from the asci.

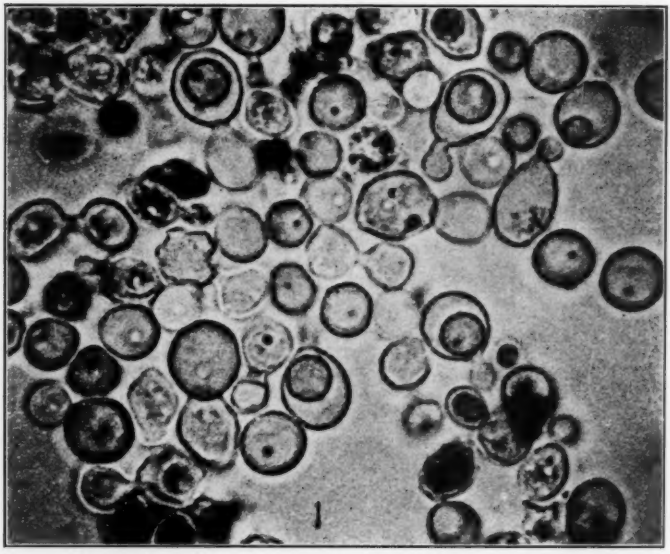

FIG. 1. Ascospores, asci and cells of *Debaryomyces Guilliermondii* var. *new zealandicus* Lodder from Garodkowa agar culture incubated at 4° C. (× 1800). The asci are much larger than the ascospores. Compare with figure 2.

The dimensions of the ascospores did not vary consistently with the incubation temperature; however, the asci and vegetative cells were slightly smaller when produced at the higher temperatures. The extent to which the ascospores filled the asci varied consistently in most instances with temperature at which they were produced (FIG. 1, 2). The asci were much larger than the spores when incubated at 4° C. but the spores nearly filled the asci when

the incubation temperature was 25° C. The effect of the incubation temperature on the relative areas of the asci occupied by the spores is shown in table II. In order to show the relative spore

TABLE II

THE EFFECT OF TEMPERATURE ON THE RATIO $\frac{\text{ASCOSPORE DIMENSIONS}}{\text{ASCUS DIMENSIONS}}$ AS MEASURED IN TWO PLANES OF 14 CULTURES OF *Debaryomyces* PRODUCED ON GARODKOWA AGAR SLANTS

Incubation Temperature Centigrade	*D. Guillier-mondii*	*D. Guillier-mondii* var. *new zealan-dicus*	*D. mem-brane-afaciens*	*D. mem-brane-afaciens* var. *hollan-dicus*	*D.* Sp. 68	*D.* Sp. 96	*D.* Sp. 101
4	——	.50×.57	.68×.69	——	——	——	——
7	.68×.81	.65×.72	.75×.75	.66×.69	.55×.60	.55×.60	.50×.55
10	.68×.78	.73×.79	.80×.80	.65×.67	.70×.70	.64×.70	.67×.67
16	.70×.81	.71×.77	.84×.84	.75×.75	.60×.67	.75×.75	.75×.75
22	.80×.80	.84×.87	.80×.80	.80×.80	.75×.75	.86×.86	.75×.75
25	No spores	.82×.84	.77×.77	No spores	——	——	——
28	No spores	No spores	No spores	No spores	.75×.86	.86×.86	.88×.88
Room	No spores	.78×.80	.84×.84	No spores	——	——	——

Incubation Temperature Centigrade	*D.* Sp. 104	*D.* Sp. 106	*D.* Sp. 108	*D.* Sp. 111	*D.* Sp. 113	*D.* Sp. 114	*D.* Sp. 115
7	.64×.70	.58×.64	.55×.65	.50×.60	.60×.60	.55×.60	.60×.60
10	.67×.67	.64×.70	.55×.55	.70×.70	.50×.55	.58×.64	.67×.67
16	.67×.75	.70×.70	.75×.75	.75×.75	.75×.75	.70×.78	.71×.71
22		.78×.78	.71×.71	.86×.86	No spores	.75×.75	.71×.71
28	.75×.75	.75×.75	No spores	.86×.86	No spores	No spores	No spores

and ascus size more clearly the data in table II are expressed as the ratio of $\frac{\text{ascospore dimension}}{\text{ascus dimensions}}$, as measured in two planes. These data show clearly that the differences in the respective dimensions of asci and spores decreased as the incubation temperature was increased.

The spores and the warty irregularities on the spore walls were easily observed at the lower temperatures, whereas at the higher temperatures the spores and the warty irregularities were not readily seen. The asci of the two cultures that sporulated at room temperature were only slightly larger than the spores.

It has been our experience that the ascospores of cultures of *Debaryomyces* grown at 16° C. or less are more readily detected than those produced at 22° C. or above, and the ascospores and

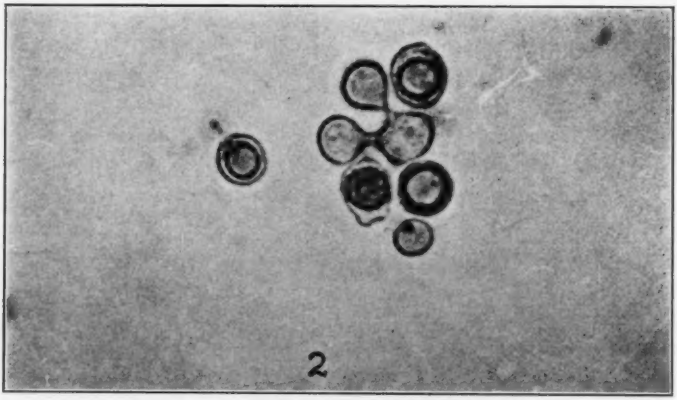

FIG. 2. Ascospores, asci and cells of *D. Guilliermondii* var. *new zealandicus* Lodder from Garodkowa agar culture incubated at 25° C. (× 1800). The ascospores and asci are much nearer the same size than those shown in figure 1.

their respective asci are more nearly of the same size from cultures grown at the higher temperatures.

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PLEOMORPHIC LIFE CYCLES IN A NEW GENUS OF THE HELOTIACEAE

W. Lawrence White and H. H. Whetzel

(with 21 figures)

Nearly every spring for the past ten years the junior author has collected or has received from other collectors specimens of certain closely related discomycetous fungi exhibiting an unusual pleomorphism and an extraordinary combination of morphological characters. During this period twenty collections have been accumulated. In the light of present evidence these seem to fall naturally into two closely related species forming a group sufficiently unlike any other known forms to justify their segregation under a new generic name. To establish this genus, and to treat of the life history, morphology, and taxonomy of the two known members is the object of the present paper. The genus seems properly to belong in the Helotiaceae of the Engler and Prantl system (**5**), in the Ciboriaceae, tribe Helotiaeae in the classification of Boudier (**1**), and in the Helotioideae of Nannfeldt (**4**).

Both species occur apparently as saprophytes, the fructifications appearing very early in the spring on a variety of plant dejecta, such as leaves, buds, and catkins, which have fallen to the ground the previous season in such moist situations as the borders of wooded swamps, the banks of forest streams, or low damp areas in mesophytic woods. There are three types of fructifications in the life cycle: apothecia, pycnidia, and spermagonia. These structures are either intermingled on the same substratum or segregated in nearby groups, and mature at precisely the same time.

A technical diagnosis of genus and species is presented at this point to facilitate later discussion.

TECHNICAL DESCRIPTION OF GENUS AND SPECIES

Pycnopeziza gen. nov. Ascocarps small, not over 5 mm. diameter, solitary or gregarious, very short stipitate to practically sessile, brown or brownish, cleistocarpous, rupturing irregularly by

fissures, or apocarpous, opening by a pore, finally saucer-shaped or flat-expanded with margin stellate or circular; hymenium waxy, light brown or buff; in section showing a thin pseudoparenchymatous hypothecium, a broad middle layer of prosenchymatous tissue, and an outside layer of small isodiametric or polygonal cells; paraphyses simple, hyaline, not forming an epithecium; asci clavate or clavate-cylindric, opening by a pore; spores small, hyaline, 1-celled, ellipsoid.

Pycnidia (*Acarosporium* Bubak & Vleugel, emend.) less than 1 mm. diameter, black or nearly so, solitary, superficial, globose or flattened-globose, attached by a broad basal portion; wall thin, pseudoparenchymatous, opening by irregular splitting from the apex toward the base, expanding widely to expose the conidial mass; conidia 2-celled, cylindric, with or without appendages, formed in dichotomously branched chains.

Spermagonia about 300–500 μ diameter, dark, solitary, scattered, attached by a short central stipe; wall thin, pseudoparenchymatous, splitting and flaking off at maturity and exposing a continuous palisade of conidiophores produced over the surface of a large central sclerotium-like core; spermatiophores simple or sparingly branched, fasciculate, septate, subcylindric, obtuse, bearing terminally small 1-celled, short-cylindric spermatia.

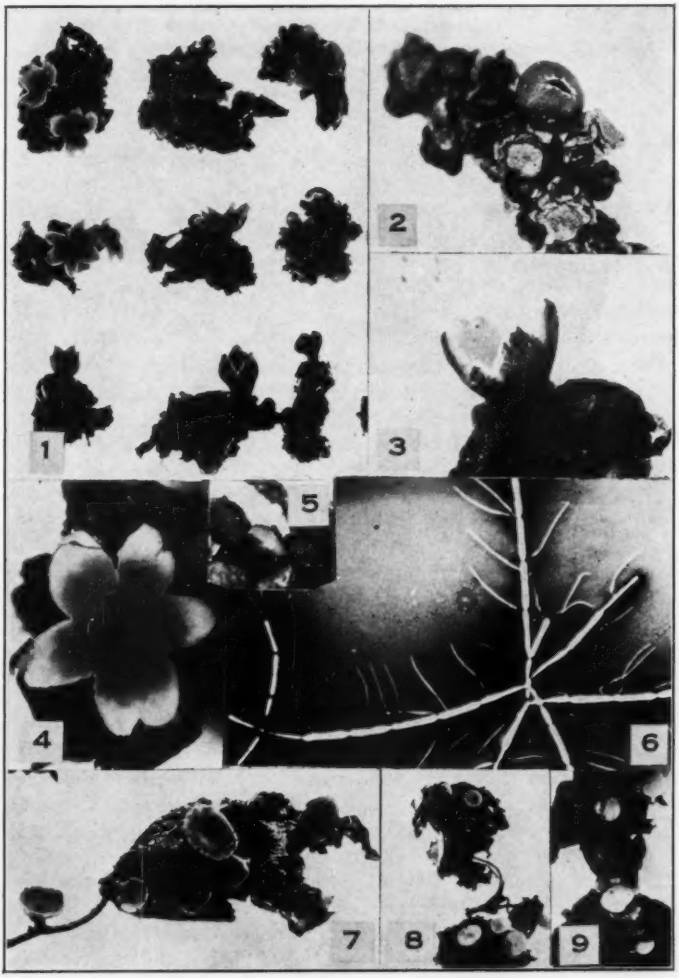
Ascomata parva, 5 mm. diametro non maiora, solitaria sive gregaria, stipite brevissimo aut subsessilia, fulva vel subfulva, aliquot fissuris sive foramine unico aperientia, ad postremum patelliformia aut plane expansa, margine stellato sive rotundato. Hymenium cereum, pallide fulvum sive argillaceum. Ascomata scissa hypothecium tenue pseudoparenchymatosum ostendentia, paginam mediam texti prosenchymatosi, externamque paginam cellularum polygonarum sive isometricarum. Paraphyses simplices, hyalinae, epithecium non formantes. Asci clavati sive clavatocylindrici, foramine aperientes. Sporidia parva, hyalina, unicellula, ellipsoidea.

Pycnidia 1 mm. diametro minora, superficialia, globosa sive leviter complanata basi lato adhaerentia. Paries levis, pseudoparenchymatosus, fissuris irregularibus ab apice versus basin aperiens. Conidia bicellula, cylindrica, appendiculis praesentibus sive absentibus, catenis dichotomis disposita.

Spermatogonia diametro circiter 300–500 μ, fusca, solitaria, sparsa, stipite brevi centralio. Paries levis, pseudoparenchymatosus, ad maturitatem squamis se findens, tapete spermatiophorum in superficie molis magnae centralis sclerotiformis detegente. Spermatiophori simplices vel raro furcati, subfasciculati, septati, subcylindrici, obtusi, in apicibus spermatia exigua, brevia, cylindrica ferentes.

Type species: *P. sympodialis*.

Type locality: Malloryville, New York.



FIGS. 1–6. *Pycnopeziza sympodialis*. 1, apothecia on buds of *Acer rubrum*, × 2; 2, apothecium showing initial rupture, × 5; 3, apothecium partially expanded, × 6 approx.; 4, apothecium fully expanded, × 8; 5, pycnidium showing initial rupture, × 8.5; 6, photomicrograph of conidial chains in crushed mount, × 370. Figs. 7–9. *Pycnopeziza quisquiliaris*. 7, apothecia, × 2; 8, same from another collection, × 1; 9, pycnidia fully opened, × 6.

KEY TO THE SPECIES

A. Apothecia opening at maturity by irregular fissures, becoming flat-expanded, stellate; surface of excipulum dark brown, minutely scabrous; conidia bearing one or more whip-like appendages ..... 1. *P. sympodialis*

B. Apothecia opening very early by a pore, becoming saucer-shaped with circular, entire margin; surface of the excipulum yellowish, minutely furfuraceous; conidia lacking appendages ..... 2. *P. quisquiliaris*

1. **P. sympodialis** (Bubak & Vleugel) comb. nov.

Syn.: *Acarosporium sympodiale* Bubak & Vleugel, Ber. Deutsch. Bot. Gesell. **29**: 385. 1911.

Apothecia small, solitary, scattered, short-stipitate, at first erect, piriform, closed, opening at maturity by splitting irregularly at the apex, followed by appearance of 4–7 fissures often extending nearly to the stipe, becoming cup-shaped to infundibuliform or campanulate, finally flat-expanded, stellate, thin, 3–5 mm. diam., lacking a sterile margin; stipe short but usually distinct, 0.5–1.5 mm. long, 1 mm. diam., narrowest at point of attachment, black, smooth, expanding above rather abruptly into the receptacle; receptacle dark brown, minutely scabrous with dark scales showing lighter color in the crevices; hymenium warm-buff to ochraceous-buff (R),[1] sometimes slightly darker in the center and typically with a slight central depression; hypothecium thin, brownish, composed of small isodiametric cells; medullary excipulum hyaline, prosenchymatous, composed of rather loosely interwoven septate hyphae 2.5–4 μ diam.; ectal layer sharply differentiated, composed of compactly arranged, polygonal, thick-walled cells, 5–7 cells thick, colorless except for the darkened exposed walls of the outer layer of cells; paraphyses simple, cylindric, colorless, 2–3 septate, 2.5 μ diam., scarcely or not at all enlarged at the apex, about same length as asci; asci 8-spored, clavate or clavate-cylindric, 75–85 $\times$ 6.5–7.5 μ, opening by a pore; spores ellipsoid or narrow-ellipsoid, sometimes slightly oblong, smooth, hyaline, 1-celled, 7–9 $\times$ 3–3.5 μ, obliquely or somewhat irregularly uniseriate.

Pycnidia (*Acarosporium sympodiale* Bubak and Vleugel) 400–1000 μ diam., solitary, scattered among the apothecia, black, globose, flattened-globose, or knob-like, attached by a broad basal portion; wall thin, soft, pseudoparenchymatous, the inner cells hyaline, the outer ones darkened, opening by an irregular slit or tear at the apex followed by the appearance of irregular fissures progressing downward from the apex, the lobes turning back

[1] R = Ridgway, R. Color Standards and Color Nomenclature. 1912.

widely to expose the white cushion-shaped mass of conidia; conidiophores produced only from the basal layer, simple, cylindric, 8–14 × 3 μ, bearing conidia terminally; conidial chains 2–3 times dichotomously branched, containing 16–20 spores from the conidiophore to the apex of any branch; conidia hyaline, cylindric, 15–22 × 2.6–3 μ, equally 2-celled, the upper cell bearing 1–3 opposite lateral appendages at approximately right angles to the spore, with an additional apical appendage on the terminal spore; appendages whip-like, typically slightly inflated near point of attachment, 26–29 × 1–1.5 μ.

Spermagonia 300–500 μ diam., solitary, scattered among the apothecia, globose or flattened-globose, seated on the substratum by a broad basal portion but actually attached only by a narrow papilla-like stalk; wall thin, pseudoparenchymatous, hyaline except for the darkened exposed walls of the outer layer; internally consisting of a large central hyaline sclerotium-like core of compactly agglutinated, thick-walled hyphae, surrounded by a very narrow spore-bearing cavity; spermatiophores subfasciculate, typically 1-septate, borne as a continuous palisade on the convex basal portion of the cavity; spermatia produced terminally, short-cylindric, 4 × 1.4 μ.

On buds and staminate inflorescences of *Acer rubrum* L., catkins of *Alnus rugosa* (DuRoi) Spreng., buds of *Populus candicans* Ait., and buds and catkins of *Populus tremuloides* Michx.; always on material produced the previous season and overwintered on the ground in moist places. Pycnidia reported on leaves of *Betula odorata* in Sweden.

New York, West Virginia, Manitoba (Winnipeg), Quebec (Burnet), Ontario (Temagami), and Sweden.

Illustrations: Bubak, Ber. Deutsch. Bot. Gesell. **29**: 383–384, text fig. 1–2; *pl. 14, fig. 1–8.* 1911. (Conidial stage only.)

HERBARIUM MATERIAL: Type specimen, Cornell University Plant Path. Herb. No. *25859,* on male inflorescences of *Acer rubrum* L., Malloryville Bog, near Ithaca, New York. Duplicate material from this same collection has been deposited in the following herbaria: Harvard University; The New York Botanical Garden; Kew Gardens, England; University of Upsala, Sweden; Bu. Pl. Ind., Washington, D. C. The following additional collections are deposited in the Plant Path. Herb., Cornell Univ. with duplicates in other herbaria as indicated:

On: Male inflorescences of *Acer rubrum*, No. *25841, 25842, 26444.*

Catkins of *Alnus rugosa*, No. *25161* (University of Toronto, Canada; State University of Iowa), and No. *25775.*

Buds of *Populus candicans*, No. *25870.*

Buds of *Populus tremuloides*, No. *24197, 25747.*

Catkins of *Populus tremuloides*, No. *25635.*

2. **P. quisquiliaris** (Ellis & Ev.) comb. nov.

Syn.: *Cyathicula quisquiliaris* Ellis & Ev. Phila. Acad. Nat. Sci. Proc. **1893**: 451. 1894.

Apothecia small, solitary or gregarious, attached by a narrow stipe-like papilla; at first globose, opening by a pore, finally saucer-shaped, rather thick, 1–4 mm. diam.; margin circular in outline, entire, obtuse, slightly elevated; stipe or stipe-like point of attachment dark brown to practically black; receptacle dotted about the base with a few small dark squamules, the upper part furfuraceous, yellowish or cream-colored; hymenium saucer-shaped, concolorous with the receptacle; hypothecium thin, brownish, composed of small isodiametric cells; medullary excipulum hyaline, prosenchymatous, the hyphae rather loosely interwoven, septate, 2.5–6 μ diam.; ectal layer sharply differentiated about the stipe-like base and there composed of compactly arranged polygonal, thick-walled cells, 8–15 μ diam., 5–7 cells thick, colorless except for the darkened exposed walls of the outer layer of cells, less well differentiated above and there composed entirely of colorless loosely arranged cells; paraphyses simple, cylindric, colorless, 2–3 septate, 2.5 μ diam., scarcely or not at all enlarged at the apex, about same length as asci; asci 8-spored, clavate or clavate-cylindric, 75–85 $\times$ 6.5–7.5 μ, opening by a pore; spores ellipsoid or narrow-ellipsoid, sometimes slightly oblong, smooth, hyaline, 1-celled, 7–9 $\times$ 3–4 μ, obliquely or somewhat irregularly uniseriate.

Pycnidia (*Acarosporium quisquiliaris*) 400–1000 μ diam., solitary, scattered among the apothecia, black, globose, flattened-globose or knob-like, attached by a broad basal portion; wall thin, soft, pseudoparenchymatous, the inner cells hyaline, the outer cells darkened, opening by an irregular slit or tear at the apex followed by the appearance of irregular fissures progressing downward from apex as lobes turn back widely to expose the pinkish cushion-shaped mass of conidia; conidiophores produced only on the basal layer, simple, cylindric, 8–14 $\times$ 3 μ, bearing conidia terminally; conidial chains 2–3 times dichotomously branched, containing 16–

20 spores from conidiophore to apex of any branch; conidia smooth, hyaline, cylindric, 15–22 × 2.6–3 μ, equally 2-celled, the terminal spore of the chain bearing a clavate-cylindric cell 7–10 × 2–2.5 μ.

Spermagonia not known.

On various kinds of overwintered bud, leaf and petiole debris of mostly undetermined species, apparently much of it of an herbaceous nature. April and May.

Iowa, New York, and West Virginia.

HERBARIUM MATERIAL: Type specimen (*Cyathicula quisquiliaris* Ellis & Ev.), "On decaying leaves, petioles, etc." Nuttalburg, West Virginia, May, 1893. L. W. Nuttall. Material of this collection in the Durand Herbarium at Cornell University and in the New York Botanical Garden Ellis Collection has been examined by the writers. The following additional collections are deposited in the Plant Path. Herbarium.

On: Buds of *Acer rubrum*, No. *25824*.

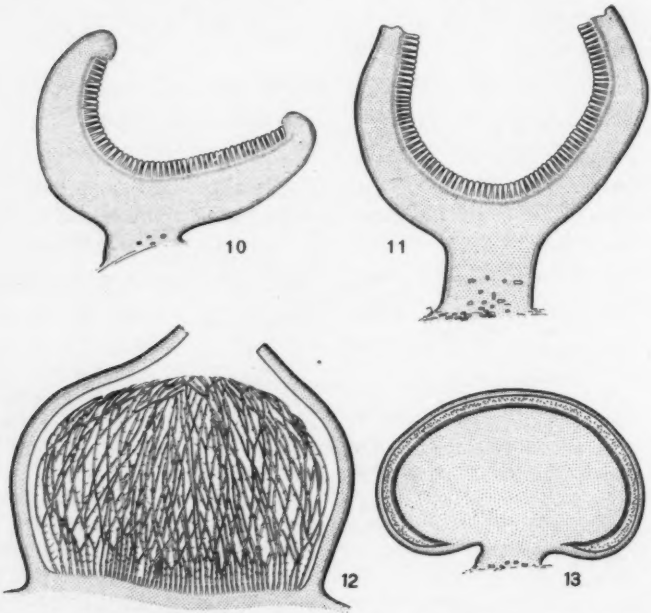
Decaying leaves of undetermined species, Nos. *15171*, *15608*, *15614*, *25743*, *25744*, *25745*, *25746*, *25892*, *25893*. Material of no. *15608* has been deposited in all of the herbaria listed for the preceding species.

ASCIGEROUS STRUCTURES

The perfect or ascigerous fruit body (FIGS. 1, 7) is in both species a small brown or brownish, almost sessile apothecium, which when fully opened is saucer-shaped, plane or repand, stellate or circular in outline, and varies in diameter from 1.5 to 5 millimeters.

The more unusual of the two species is *P. sympodialis*, in that the ascigerous fructification is a cleistothecium. This ruptures at maturity by four to seven irregular radiating fissures starting at the apex (FIG. 2) and progressing about two-thirds of the way to the stipe (FIG. 3), so that on expanding it presents such an appearance as would be given by a minute *Geaster* (FIG. 4) from which the gleba and endoperidium had been removed. Before opening, the fruit body has the appearance of a small, brown, short-stipitate, piriform puffball. The fissures form irregularly, there being no

predetermined point or line of dehiscence (FIG. 2). The cavity of the mature but unopened ascocarp is lined throughout, top as well as sides and bottom (FIG. 11), with the hymenium, the asci being largely mature and ready to discharge spores at the time of rupture. In this species there is no peripheral growth following



FIGS. 10–13. Diagrammatic representations of the various types of fruit bodies in the genus *Pycnopeziza* as seen in freehand sections. Drawn with aid of camera lucida. 10, *P. quisquiliaris*, apothecium, not yet fully expanded, × 17. Figs. 11–13, *P. sympodialis*, 11, apothecium just after rupturing, × 17; 12, pycnidium, just after rupture of the wall, showing position of conidiophores and conidial chains, × 64; 13, spermagonium, showing position of the spermatial cavity and spermatiophores, × 64.

the opening of the apothecium. Consequently the sterile margin formed by extension of the excipular hyphae beyond and often above the ascus layer, which is characteristic of the usual cupulate or discoid apothecium, is lacking in this case. Instead, the hymenium and its supporting hypothecial and excipular tissues terminate abruptly at the periphery (FIGS. 3, 11), and exhibit, until

the time of extreme maturity and disintegration, the irregularly broken wall as it was left at the time of rupture.

P. quisquiliaris (FIGS. 7, 8) follows the more usual course of development, an apical pore appearing at a very early stage and continuing to enlarge with lateral expansion and marginal growth of the disc. During this process the paraphyses are formed, and finally the asci push up among them to form the hymenium on the open, exposed inner surface. This type of opening is typical of the large group of fleshy cupulate or discoid species comprising the Helotiaceae and Mollisiaceae of the Engler and Prantl system.

Immediately underlying the hymenium in both species (FIGS. 10, 11) is a thin, brownish, pseudoparenchymatous hypothecium. Beneath this layer is the much thicker, hyaline, prosenchymatous medullary excipulum of rather loosely interwoven septate hyphae. This middle layer is in turn enclosed by a more or less well developed ectal layer of small isodiametric cells and is about five to seven cells (40 to 50 μ) thick. In *P. sympodialis* the exposed walls of the outer layer of cells are dark brown and thickened, and minute crevices appear between them, thus imparting a minutely scabrous appearance to the outside of the apothecium (FIG. 3) both before and after opening. In *P. quisquiliaris* a few such darkened cells appear about the basal portion of the receptacle (FIG. 10), but aside from this the entire outer surface of the disc is a creamy yellow or clay-color, more or less concolorous with the hymenium, and is minutely furfuraceous under a lens. In section the ectal layer of the excipulum is seen to be composed of rather loosely arranged colorless cells formed by the septation of hyphal tips that have turned outward from the medullary layer. The shape, color and excipular markings of the mature apothecia always serve to distinguish the two species in the field. The stipe of *P. sympodialis* is short, black, not over 1.5 mm. long, about 1 mm. in diameter, and tapers slightly toward the point of attachment; in *P. quisquiliaris* the stipe is practically wanting.

The hymenial elements (FIG. 16) in the two species are in no way striking, being typical of those found throughout such genera as *Ciboria, Sclerotinia,* and *Helotium.* The paraphyses are simple, one- to three-septate, and barely clavate at the apex. The asci are clavate or clavate-cylindric, eight-spored, and discharge their spores

through an apical pore. The spores are small, hyaline, one-celled, ellipsoid, the arrangement being uniseriate or rarely sub-biseriate.

PYCNIDIAL STRUCTURES

Had this stage of the fungus been found unassociated with the perfect stage its characters would have placed it in the family Excipulaceae. The pycnidia, which except for spore characters are alike in the two species, begin development subepidermally, become erumpent very early, and at maturity appear as scattered, dark brown or practically black, minutely scabrous, flattened-globose or knob-like structures (FIG. 12) less than one millimeter in diameter. They are attached to the substratum by a broad, slightly constricted basal portion. Structurally this underlying wall consists of a thin, subhyaline, pseudoparenchymatous, cushion-like tissue resting on the surface of the substratum (FIG. 12). At the periphery of this layer, and continuous with it, arise the sidewalls, which are thin and of a similar pseudoparenchymatous character. The innermost cells are hyaline. Toward the outside they are yellowish or brownish with the exposed walls of the outer layer black. Sometimes minute fissures appear between the cells so as to present a minutely scabrous appearance under a lens.

The conidiophores (FIGS. 14, 15) are simple, cylindric, hyaline, single-celled, and stand side by side (FIG. 12) in a continuous palisade layer on the basal cushion. The sidewalls of the pycnidium are sterile. The conidia are hyaline, cylindric, equally two-celled, and are firmly joined end to end in one- to three-times dichotomously branched chains. The chains are from sixteen to twenty spores in length.

In *P. sympodialis* each conidium bears one, two, or three lateral whip-like appendages (FIGS. 6, 15, 19) on the apical cell of the spore. The terminal spore of the chain bears in addition an apical appendage. When an intercalary conidium has more than one appendage they are borne on opposite sides of the spore. The spores of a given collection usually have one, two, or three appendages with intermediates typically lacking.

In *P. quisquiliaris* the intercalary conidia lack appendages (FIG. 14), while the terminal spore of the chain bears a clavate-cylindric

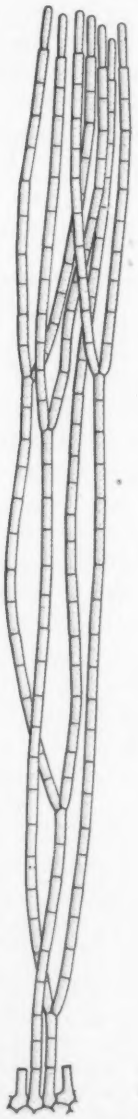


FIG. 14. *Pycnopeziza quisquiliaris.* Chains of 2-celled conidia. × 560.

cell of about two-thirds the diameter and about two-thirds the length of the conidium.

At maturity the pycnidium ruptures irregularly (FIGS. 5, 9) with the lobes turning out and down toward the substratum in a star-like fashion, thus exposing the subglose, gelatinous, white or slightly reddish mass of conidia (FIG. 9). With extreme maturity the chains disintegrate and the conidia are washed out by rain leaving the old, flattened and spreading, star-shaped peridium.

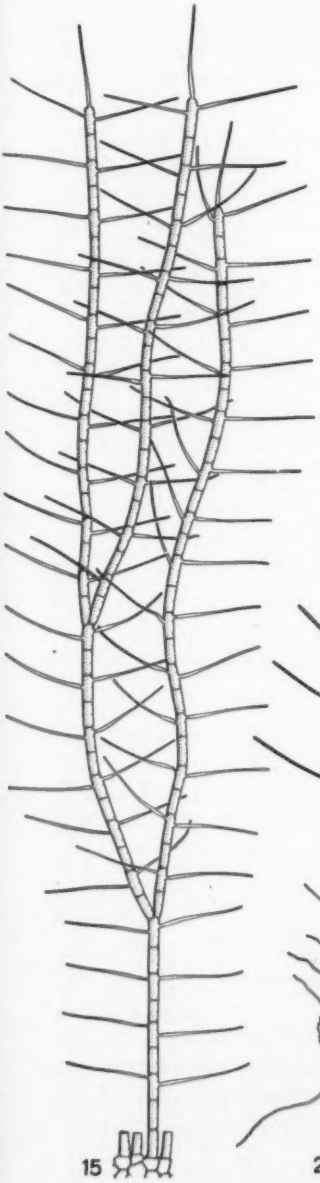
SPERMAGONIAL STRUCTURES

Spermagonia have been found only in *P. sympodialis*.

In external appearance the spermagonium resembles closely the unopened pycnidium. It is, however, attached to the substratum by a very short central stipe (FIG. 13). The latter character can be observed only in sectional view because the basal portion is usually in contact with the substratum and on superficial observation the sidewalls appear to arise as in the pycnidium.

The structure of the young spermagonium is essentially that of a sclerotium. It consists of interwoven, short-celled, thick-walled hyphae surrounded by a rind of small, isodiametric, thick-walled cells (FIG. 21) and is four to six cells thick. The exposed walls of the outermost layer of cells are blackened so as to give a dark color to the structure. This outer cellular layer is not unlike that of the apothecium and pycnidium. Just inside the rind of the maturing spermagonium, and entirely surrounding the large central sclerotium-like core except over the basal area, is a very narrow cavity (FIG. 13) lined on the inner surface with a continuous palisade of minute, subcylindric, simple or forked fasciculate spermatiophores (FIG. 21). A crosswall at the base cuts off the spermatiophore, which often exhibits a septum between this point and the apex. Small, one-celled, cylindric spermatia are produced terminally.

FIGS. 15–21. *Pycnopeziza sympodialis*. 15, conidial chain of the biflagellate form of the species, × 445; 16, asci with spores, and paraphysis, × 900; 17, ascospores germinating in drops of distilled water, × 680; 18, ascospores germinating on two percent potato dextrose agar, × 680; 19, triflagellate form: two mature conidia at the apex of the chain with the terminal conidium in the process of formation, × 680; 20, conidia germinating in drops of distilled water, × 680; 21, section through spermatial cavity showing spermatiophores, spermatia, and spermagonial wall, × 900.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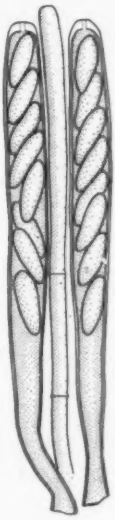
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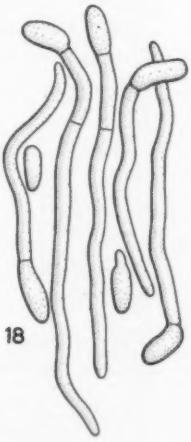
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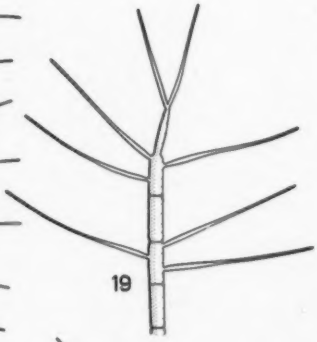
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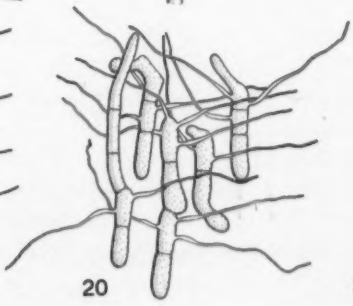
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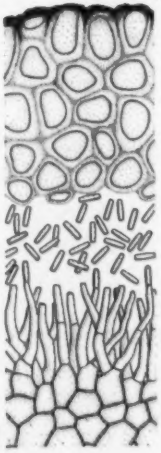
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NOTES

Bubak (2) in 1911 described and figured the pycnidial stage of *P. sympodialis*. For this he established in the Excipulaceae the genus *Acarosporium* Bubak & Vleugel based on *A. sympodiale*. The material upon which Bubak's paper is based consisted of a single collection taken in Sweden by Mr. J. Vleugel who sent the specimen to Bubak in Czechoslovakia for determination. The pycnidia are described as occurring on the under surface of the previous season's dead leaves of *Betula odorata*. If apothecia or spermagonia were present in the collection Bubak evidently either did not find them or else failed to recognize them as different stages in the same pleomorphic species, for there is no mention in his paper of such structures.

Though the writers have not seen Bubak's material, the form is so characteristic that there can be little or no doubt as to its identity. Bubak describes the conidia as having typically only one appendage with two or sometimes three being present on the apical spore. The first collection of the species to come into the hands of the writers would match Bubak's material exactly in this respect. However, as more collections were secured some were found to have conidia constantly bearing two appendages. In the Spring of 1936 a collection taken near Morgantown, West Virginia, on *Alnus* catkins showed conidia constantly biflagellate. Material taken in the same locality under the same *Alnus* shrubs in the Spring of 1937 had intercalary conidia bearing typically three appendages per spore and as many as four or five on the apical spore. The obvious conclusion, especially since there are no correlated differences in the perfect stage, is that these represent merely variations in the same species.

The second species, *P. quisquiliaris*, is maintained on the basis of total absence of flagella on the conidia, correlated with differences in the ascocarp striking enough to enable one to easily distinguish the two forms in the field.

It should be pointed out here that in *P. sympodialis* the appendages, according to Bubak (2), play a very important part in a unique process of acropetalous conidial formation, which is described and illustrated in some detail in Bubak's paper. Bubak's

form genus, *Acarosporium*, is here redescribed and emended to include the additional forms that must be placed there.

CULTURE WORK

In *P. sympodialis* both ascospores and conidia germinate on potato dextrose agar within a few hours and produce a rapid-growing mycelium. The ascospores first produce a germ tube from one end of the spore (FIG. 18), but after this has reached a length of 500–600 μ another is produced from the opposite end. The conidia produce two germ tubes, one from each end of the spore, either simultaneously, or one following the other as in the ascospores. The germ tubes of both ascospores and conidia are essentially alike. They are regular in diameter, 3.5–5 μ, slightly flexuous, becoming septate and finally branch sparingly and at wide angles. Single ascospores produce a mycelial growth approximately 4 cm. in diameter within six days. Up until this time the growth has been medium dense, white, with considerable fine aerial mycelium and a regular, finely radiating margin. Some olive color now develops about the center of the growth and the entire mycelial mat rapidly becomes dark olive and finally black. Cultures from ascospores and from conidia are very much alike, although in general it may be said that those resulting from the former are somewhat thicker and heavier than the latter, and more radiating in appearance.

In drops of distilled water ascospores and conidia behave in much the same manner. Many of the ascospores become septate (FIG. 17), and many of the conidia form a septum (FIG. 20) in the middle of each cell. Germination seldom results and when it does occur the germ tubes remain short.

Pycnidia have been produced from mass ascospore plantings and from mass conidial plantings at 15° C. on potato dextrose agar streilized together with *Populus* buds and with *Alnus* catkins. They did not appear on a similar medium or on plain potato dextrose agar held at room temperature, nor did they occur on potato dextrose agar at 15° C. However, it should be noted at this point that no great amount of culture work has been done. The pycnidia and their conidia developed in culture did not differ from those produced in the field.

Recent ascospore cultures of *P. quisquiliaris* have not been avail-

able, so that the two species have not been grown side by side for comparison. No collections of *P. quisquiliaris* have been made during the last two years. Stock cultures of the two species show no noticeable differences.

DISCUSSION

There can remain no doubt as to the genetic connection of the different types of fruit bodies here described as occurring in the life cycle. Both apothecia and pycnidia are present on all, except one, of the eighteen collections examined, including the Ellis and Everhart type of *P. quisquiliaris*. In addition, typical pycnidia have been produced in culture from ascospores. Spermagonia have not appeared in culture. While not yet found in *P. quisquiliaris*, the spermagonia have been present in several collections of *P. sympodialis*, where, in addition to being scattered among the apothecia, they sometimes occur as pouches on the apothecial stipe or on the under side of the apothecium where they occur as outgrowths from the underlying tissue. In some instances there is no indication whatever of any central pycnidial core, but instead the spermatiophores arise directly from the medullary excipulum of the apothecium from which the ectal layer becomes loosened, forming a spermatial cavity similar to that in the normal spermagonium.

The manner of opening of the ascocarp in *P. sympodialis*, which seems to correspond closely to that of the operculate species, *Urnula Geaster* Peck, is probably of little significance as an indication of taxonomic position, since the species is obviously closely related to the more typical *P. quisquiliaris*. The genus would seem to have very little in common with *Cyathicula*, where *P. quisquiliaris* was placed by Ellis and Everhart (**3**).

The occurrence in *Pycnopeziza* of the three types of fructifications at the same time of year seems worthy of special mention here as being of very rare occurrence.

Shear and Dodge (**6**) give an account of the life history and morphology of a Discomycete which they discuss under the name *Pezizella Lythri* (Desm.) Shear & Dodge. A close parallelism is apparent between that fungus and the organisms discussed in this paper, but the two could scarcely be considered congeneric in respect to similarity of any of their fruiting structures.

We are under many obligations to Dr. G. R. Bisby, formerly of the University of Manitoba, and to Dr. C. R. Orton of the University of West Virginia for courtesies and assistance on our collecting trips to their respective localities where excellent materials of these fungi were obtained; also to Dr. G. W. Martin of the University of Iowa for collections of *P. quisquiliaris;* to Dr. F. L. Drayton and his colleagues for records of *P. sympodialis* in eastern Canada; to Dr. H. M. Fitzpatrick who has kindly assisted by a critical reading of the manuscript; and to Mr. W. R. Fisher who made all the photographs except that used in figure 4, which was supplied by Mr. T. Sproston. The drawings were made by the senior author.

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THE GENUS AGARICUS IN WESTERN WASHINGTON [1]

J. W. Hotson and D. E. Stuntz

(with 12 figures)

This article is the third of a series dealing with the little-known Agaric flora of Washington. Two previous papers (**8, 9**) have discussed the Amanitae of this State, and the present one will concern the genus *Agaricus*. This genus is well represented in the Pacific Northwest, but when one wishes to identify collections made in this region, he faces an obstacle in the lack of available information concerning the local flora, and also in the fact that some of the species occurring here are more closely allied to European forms than to those found in the eastern United States. In the following article an attempt is made to bring together the scattered information regarding the genus *Agaricus* as it occurs in western Washington, to add some few new facts, and to assemble all the species reported for this region into a usable key, with brief comments on each species. It is hoped that the information thus accumulated may form the basis of a more extensive study of the genus. Although most of the species dealt with have been found in the Puget Sound area, some few from the adjacent areas of Oregon and British Columbia have been included where it has seemed probable that they also occur in Washington.

Collections can usually be referred without much doubt to the genus *Agaricus*, as it is a well defined, homogeneous group, strikingly free from those troublesome species which show a transition to neighboring genera. But to be sure of the species is quite a different matter. Not only do many of the species resemble each other very closely in size, color, and general outward appearance, but there is little in the way of microscopic characters which can

[1] The use of the genus name *Agaricus* instead of *Psalliota* is in accordance with the "International Rules of Botanical Nomenclature," 1935, p. 15, Sect. 8, Art. 51, and p. 123.

be used to distinguish them.[2] To further complicate matters, the student will often find a lack of agreement among mycologists concerning the interpretation of a particular species, and is apt finally to be more confused than helped by the literature he consults. This condition has been found as prevalent in Europe as in America.

In the key no attempt has been made to show natural relationships between the species. It has been deemed more advisable, in view of the inherent difficulties of the genus, to construct a key, however artificial in nature, which will, above all, facilitate the identification of the species found. In the main, characters have been used which are readily recognizable and as definite as possible. An attempt has been made to use sparingly such variable or indefinite characters as habitat, size, or double annulus. Concerning the last, a word of explanation may save some confusion. The writers consider as a true "double" annulus one which is composed of two definite concrescent layers, the upper derived from the partial veil, the lower from tissue which was continuous between the stem and the surface of the pileus while the latter was yet unexpanded. This lower layer usually cracks into conspicuous radial patches on the under surface of the membranous partial veil, and such a structure is, when fully developed, a readily recognizable feature. But unfortunately, there are intergradations between the typical double annulus and the typical one-layered single annulus, and the degree of evident "doubleness" may even vary somewhat in the same species. Hence this character is not always an infallible means of recognizing the species which have it.

It has been found difficult at times to express in the form of a key the exact differences which constitute the distinguishing characteristics of a species. To avoid this difficulty the usual form of a skeleton-key has been combined with a sufficiently full description of the species so that one may be able to determine his species without going to the trouble of consulting a technical description which always is time-consuming.

[2] Lange (13) has pointed out that the presence or absence of sterile cells on the edge of the gills is of some taxonomic value. Drawings of some of these cells are shown in figure 1.

AGARICUS Fries, Syst. Myc. **1**: 8. 1821, emend. Karst. Hattsv. **1**: 482. 1879

(*Psalliota* Fries)

Pileus fleshy, putrescent, surface silky and smooth to fibrillose or scaly, seldom viscid; *gills* free, thin and crowded, edge often heteromorphic; *stem* fleshy-fibrous, central, its context distinct from the trama of the pileus, and hence readily separable from the latter; *annulus* present; *volva* lacking; *spores* purple-brown or fuscous-purple in mass, smooth, without an apical germ pore; *habitat* terrestrial in lawns, meadows, or cultivated places, less frequently in the woods.

In structure this genus resembles *Lepiota* among the white-spored forms, and *Chamaeota* among the pink-spored. The closest genus of the purple-brown-spored group is *Stropharia*, which differs in having adnate gills, stem confluent with the pileus, and spores usually with a prominent germ pore.

A KEY TO THE SPECIES

A. Mature pileus less than 5 cm. broad

B. Pileus with pink or rose-red scales on a grayish-white surface, 4 cm. broad, convex or plane, staining yellow where touched, flesh thin, white, odorless and tasteless; *gills* ventricose, moderately broad, close, edges entire, soon becoming grayish or purplish-gray then black; *stem* 3–4 cm. long, 3–4 mm. thick, equal, base slightly bulbous, stuffed then hollow, satiny smooth, white, staining yellow where touched; *annulus* superior, small, pendant, simple, thin as tissue paper but persistent, white; *spores* 6.5–7 × 4–5 μ.

1. *Agaricus diminutivus* Peck

BB. Pileus without pink or rose-red scales

C. Pileus convex, not umbonate; all parts of the sporophore staining deep yellow where bruised; stem short, stout, solid, 4 cm. long, 8 mm. thick, glabrous, white; *pileus* 4.5 cm. broad, innately fibrillose or with few minute appressed scales, center brown, elsewhere pallid or whitish, flesh thick, white, unchanging; *gills* broad, thin, crowded, long white, becoming pink then purplish gray; *annulus* median or inferior, narrow, thin, simple, persistent, white; *spores* 5–6 × 4–4.5 μ ... 2. *Agaricus micromegethus* Peck

CC. Pileus umbonate; no part of the sporophore staining yellow where bruised; stem slender

D. Pileus white with brownish center, with innate purplish fibrils, 3 cm. broad, umbonate, smooth, flesh white, with

pleasant odor and sweetish taste; *gills* ventricose, narrow, somewhat crowded, pale gray with brownish tinge; *stem* 4–5 cm. long, 3–4 mm. thick, base bulbous, fibrillose, white, flesh yellowish; *annulus* median, narrow, erect, simple, thin, persistent, white; *spores* 5 × 3 μ .. 3. *Agaricus dulcidulus* Schulz.

DD. Pileus lacking innate purplish fibrils, and not white with brownish center

E. Pileus and stem uniformly pale avellaneous; *pileus* truncate-conic to convex with a large umbo, not fully expanding, drying thin, 4 cm. broad, surface minutely imbricate-fibrillose, dry, uniformly pale avellaneous throughout; *gills* free, crowded, ventricose, becoming fuliginous; *stem* enlarging below, with very small bulb, subconcolorous, minutely fibrillose, 6 cm. long, 4–6 mm. thick; *annulus* superior, simple, fixed, persistent, white; *spores* ellipsoid, smooth, purplish-brown, 5 × 2.5 μ.

4. *Agaricus bivelatoides* Murr.

EE. Pileus rosy-buff, center darker, stem white below, pink above; *pileus* small, thin, conic to convex, umbonate, solitary, 3 cm. broad, surface rosy-isabelline to whitish, pinkish-brown to fulvous on the umbo, dry, slightly fibrillose-scaly, margin entire, concolorous; *gills* free, crowded, plane, becoming fuliginous; *stem* smooth, polished, enlarged below, becoming yellowish throughout on drying, 7 cm. long, 4 mm. thick above, 8 mm. thick below; *annulus* white to yellow, membranous, ample, persistent, fixed just above the middle of the stipe; *spores* ellipsoid, smooth, pale-purplish under a microscope, 5 × 2.5 μ ..... 5. *Agaricus comptuloides* Murr.

AA. Mature pileus more than 5 cm. broad

F. Flesh of all parts quickly becoming red or reddish-brown where bruised

G. Pileus white, 8 cm. broad, with obscure appressed squamules faintly tinged grayish-brown, convex, flesh thick, firm, white, quickly becoming blood-red where bruised; *gills* remote, rounded at stem, pointed at margin, ventricose, close, 8 mm. broad, russet-vinaceous (R); *stem* 13 cm. long, 1 cm. thick, equal, base slightly bulbous, solid, surface satiny, white, brownish below; *annulus* superior, narrow, flaring then pendant, simple, membranous, persistent, white; *spores* 5–7 × 3.5–4.5 μ.

6. *Agaricus albosanguineus* sp. nov.

GG. Pileus with conspicuous brown scales

H. Stem long and slender, hollow, solid at the base which is sometimes bulbous, 4–8 cm. long, 6–12 mm. thick, cylindrical,

silky or fibrillose, white becoming darker; *pileus* 5–10 cm. broad, convex, at first flocculose then with concentric, broad, appressed scales, reddish-brown, flesh white or pale alutaceous, immediately becoming blood-red where broken, odorless and tasteless; *gills* approximate, rounded at stem, ventricose, white then rosy finally purplish umber; *annulus* superior, large, simple, membranous, edge often lacerate, persistent, white to alutaceous; *spores* 5–7 × 3–4 μ.

7. *Agaricus haemorrhoidarius* Fries

HH. Stem short and stout, solid, equal, base not bulbous, 4–5 cm. long, 2 cm. thick, smooth, pallid or white; *pileus* 10 cm. broad, plane or convex, with broad, appressed brown scales, flesh thick, compact, whitish, immediately becoming reddish-brown where bruised, odor and taste not marked; *gills* very closely approximate, rounded at stem, pointed at margin, ventricose, broad, crowded, at length becoming dark purplish-brown; *annulus* nearly median, narrow, pendant, thick, persistent, felt-like; *spores* 7 × 4.5–5 μ.

8. *Agaricus halophilus* Peck

FF. Flesh not changing quickly to blood-red or reddish-brown where bruised (Gradual darkening of exposed flesh may take place, or the flesh may become yellow)

I. Mature pileus with conspicuous colored scales which are darker than their background: never white or whitish

J. Lower surface of annulus bearing conspicuous warts, scales or patches (double annulus)

K. Pileus vinaceous or purplish-brown, 7–9 cm. broad, with many small, hairy areolae, convex, flesh white, odorless, taste bitterish or nauseous; *gills* somewhat remote, narrow, crowded, edges entire, pink becoming purple-brown; *stem* 8–12 cm. long, 1 cm. thick, equal, base clavate, hollow, context vinaceous, surface below annulus with white floccose scales; *annulus* superior, moderately large, deflexed, double, thick, under surface floccose-scaly, becoming vinaceous; *spores* 5–6 × 3 μ ..... 9. *Agaricus subrutilescens* Kauff.

KK. Pileus without vinaceous or purplish-brown color

L. Stem glabrous: annulus without yellowish or ochraceous floccose areolae on under surface; spores less than 7 μ long (except N.)

M. Annulus with under surface radially cracked into thick, stellate patches; pileus with minute blackish-brown scales which are denser toward the center, 8–15 cm. broad, plane, flesh thick, white, becoming yellowish and later reddish-

brown when bruised, odorless; *gills* approximate, rounded at stem, pointed at margin, narrow, crowded, pallid then pink, finally purple-brown; *stem* 8–16 × 1.5–3 cm., equal, base sometimes bulbous, hollow, satiny smooth, white; *annulus* superior, ample, pendulous, white; *spores* 4.5–6 × 3–3.5 μ ..... 10. *Agaricus placomyces* Peck

MM. Annulus without thick stellate patches; scales of pileus not blackish-brown

N. Pileus with reddish-brown scales, nowhere straw-colored, nor becoming yellow on drying: stem long, slender, 8–10 cm. long, 1–1.5 cm. thick, equal, hollow, glabrous, white, base bulbous and often yellow; *pileus* 8–10 cm. broad, convex, often somewhat umbonate, densely scaly, scales and center reddish-brown to fuscous, flesh white, odor and taste pleasant; *gills* equally narrowed at both ends, crowded, white then rosy flesh-color finally reddish-brown; *annulus* membranous, superior, ample, pendant, under surface flocculose, white; *spores* 6–8 × 3–4 μ.

11. *Agaricus silvaticus* Schaeff.

NN. Pileus with straw-colored margin and fulvous center, becoming yellow on drying; stem short and stout; *pileus* hemispheric to broadly convex, not umbonate, drying thin, gregarious, 6 cm. broad, surface dry, smooth, imbricate-fibrillose-scaly, fulvous with a latericeous tint at the center; *gills* free, ventricose, not crowded, avellaneous to umbrinous; *stem* cylindric, slightly larger at the base, smooth, glabrous, white above the annulus, ochraceous-tinted below, 5 cm. long, 1 cm. thick; *annulus* ample, membranous, persistent, fixed about the center of the stipe, white, changing to yellow on drying; *spores* ovoid, smooth, purplish-brown, 4–5 × 3–4 μ.

12. *Agaricus flavitingens* Murr.

LL. Stem floccose or scaly below the annulus; annulus with conspicuous yellowish or ochraceous floccose areolae on the under surface; spores more than 7 μ long

O. Pileus without any tinge of yellow or straw color, 10–20 cm. broad, convex then plane, with many tiny, appressed, tawny scales on a white background, flesh thick, white, bruising tawny; *gills* remote, ventricose,

narrow, crowded, white then pink, finally purple-brown; *stem* 15–25 cm. long, 2–2.5 cm. thick, equal, base not bulbous, stuffed then hollow, white, staining yellow then brown where bruised; *annulus* superior, very large, with brownish floccose patches on the under surface; *spores* 7.5–9 × 5–6 μ.

13. *Agaricus subrufescens* Peck

OO. Pileus with a definite yellow or straw-colored tinge

P. Stem shorter than or equal to the width of the pileus, 9–15 cm. long, 2.5–5 cm. thick, solid, densely squarrose below the annulus, yellowish or ochraceous; *pileus* 8–18 cm. broad, convex, with small appressed auburn scales, staining yellow where bruised, flesh thick, white, bruising reddish-brown; *gills* narrow, ventricose, extremely crowded, becoming purplish-brown; *annulus* superior, very thick and broad, under surface densely floccose-areolate, yellowish; *spores* 8–10 × 5–6 μ .... 14. *Agaricus villaticus* Brond.

PP. Stem longer than the width of the pileus

Q. Spores 7–13 × 5–6 μ; gills never pink, pallid, becoming chocolate or fuscous, remote, narrow, crowded; *pileus* 10–20 cm. broad, convex, silky, straw-colored, covered with appressed brown scales, flesh white, soft, odor of anise; *stem* 6–20 cm. long, 1.5–5 cm. thick, tapering upward, floccose below the annulus, white, becoming yellow then brown where bruised; *annulus* superior, ample, pendant, double, white, with yellowish, floccose areolae on the under surface.

15. *Agaricus augustus* Fries

QQ. Spores 7–9 × 4–5 μ; gills soon bright pink, at length fuscous-purple, remote, rounded at stem, pointed at margin, crowded, not broad; *pileus* 10–15 cm. broad, convex, straw-yellow, covered with fulvous scales, flesh white, odor faintly of anise; *stem* 9–15 cm. long, 1.5–3 cm. thick, equal, base bulbous, hollow, floccose-scaly below annulus, white and smooth above; *annulus* superior, ample, pendant, double, persistent, white and smooth above, with yellowish floccose scales below . 16. *Agaricus perrarus* Schulz.

JJ. Annulus membranous, the under surface entirely devoid of scales, warts, or patches (simple annulus)

R. Pileus with large, broad, brown scales, often diffracted-scaly; annulus slight, lacerate, evanescent or deciduous; plants of medium size, up to 8 cm. broad

S. Annulus deciduous; gills never bright pink; pileus grayish or avellaneous with large scales, 5–7 cm. broad, convex, flesh thick, white, unchanging, odor anise-like; *gills* approximate, rounded at stipe, acuminate at margin, narrow, crowded, pallid, then grayish-pink, finally purple-brown; *stem* 5–6 cm. long, 1 cm. thick, equal, base incrassated, stuffed, glabrous, grayish to avellaneous; *spores* 6–8 × 4–5 μ.

17. *Agaricus pratensis* Schaeff.

SS. Annulus not deciduous, sometimes evanescent; gills soon becoming and long remaining bright pink; pileus white, only the scales avellaneous; in other particulars like the typical form (See under **X.**)

21. *Agaricus campestris* Fries

RR. Scales of the pileus small, tawny or fuscous; annulus persistent, entire; large plants, 10 cm. or more in width, with proportionate height

T. Annulus narrow, collar-like; scales small, scattered, fuscous; flesh bruising yellow; gills vinaceous-fawn from the first, never becoming pink, at length purple-brown, moderately broad, crowded; *pileus* 10–20 cm. broad, convex, with appressed, fibrous scales, odor and taste pleasant; *stem* 8–17 cm. long, 2–3.5 cm. thick, subequal, base slightly bulbous, hollow, glabrous, whitish-gray to mouse-gray, becoming reddish-brown when handled; *annulus* superior, simple, persistent, white, becoming brownish when bruised; *spores* 5–6 × 4 μ ..... 18. *Agaricus cervinifolius* Zeller

TT. Annulus broad, pendant; scales densely imbricated, tawny; flesh never staining yellow; gills becoming pink as they develop

U. Base of stem bulbous, often yellow; (for remainder of description, see **N.** above)

11. *Agaricus silvaticus* Schaeff.

UU. Base of stem not bulbous, not yellow; *pileus* convex to sub-expanded, slightly umbonate, thick and fleshy, solitary, reaching 10 cm. broad, surface dry, smooth, whitish, densely covered with imbricate, delicately fibrillose, rufescent scales, ex-

cept at the center, where it is glabrous and fulvous to bay; *gills* free, rather close, ventricose, pallid to pale-purplish; *stem* tapering upward, not bulbous, glabrous, white, staining slightly reddish-brown when bruised, 7 cm. long, 1–1.5 cm. thick; *annulus* ample, membranous, simple, white, staining slightly reddish-brown, fixed, superior; *spores* narrowly ellipsoid, obliquely pointed at the base, smooth, pale purplish-brown, 6–7 × 3.5 μ.

19. *Agaricus subrufescentoides* Murr.

II. Mature pileus silky smooth or fibrillose, white or pallid, without evident scales of a darker color

V. Annulus flaring, collar-like, with two separate edges, thick, double, floccose below, median, narrow, persistent, white; *pileus* 8–18 cm. broad, semiglobose to convex, smooth, glabrous, white with ochraceous center, flesh very thick, white, unchanging, odor pleasant; *gills* approximate, rounded at the stem, ventricose, narrow, crowded, white then grayish vinaceous, finally purple-brown; *stem* 6–11 cm. long, 2.5–5.5 cm. thick, equal, base not bulbous, stuffed, tomentose below the annulus, smooth above, white; *spores* 6–7.5 × 4.5–5 μ.

20. *Agaricus Rodmani* Peck

VV. Annulus not having two separate flaring edges

W. Annulus simple, with no scales or patches on the lower surface; no part of the sporophore staining yellow where bruised

X. Annulus lacerate, small; pileus entirely white, 5–8 cm. broad, convex, smooth, white, flesh thick, white, unchanging, odor and taste pleasant; *gills* approximate, rounded at the stem, ventricose, narrow, crowded, very soon bright pink, finally purple-brown; *stem* 5–6 cm. long, 1–2 cm. thick, equal or tapering downward, solid, glabrous, white; *annulus* median or superior, narrow, flaring then pendant, thin, white, often evanescent; *spores* 7.5–10 × 4.5–6 μ . 21. *Agaricus campestris* Fries

XX. Annulus entire, large; pileus with grayish-brown center, regular, convex, thick and fleshy, solitary, 5–10 cm. broad, surface smooth, dry, subglabrous, white, becoming pale bay at the center on drying, margin thin, entire, decorated with fragments of the veil, context white to slightly pinkish, not changing, with pleasant taste and odor; *gills* free, crowded, broad, ventricose, pink to fuliginous; *stem* bulbous, tapering upward, smooth, glabrous, white, pinkish above the annulus, stuffed or hollow, 7–10 cm. long,

8–12 mm. thick; *annulus* superior, simple, white, large, persistent; *spores* ellipsoid, smooth, purplish-brown under a microscope, 5–6 × 3.5 μ.

22. Agaricus Hillii Murr.

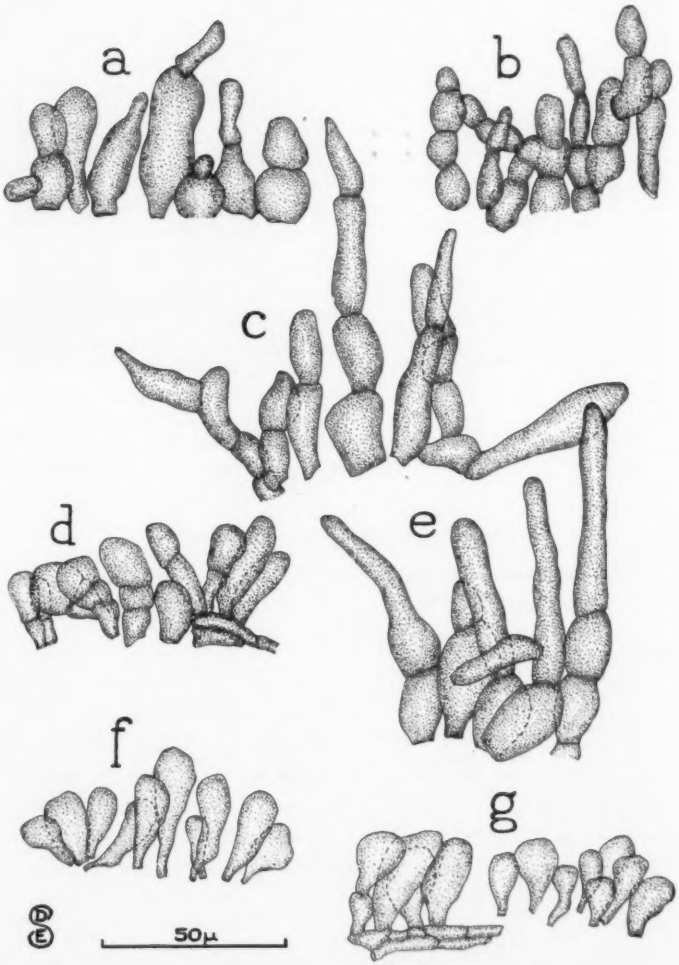

FIG. 1. Camera lucida drawings of sterile cells on the edge of the gills: *a, A. augustus; b, A. perrarus; c, A. arvensis; d, A. silvicola; e, A. villaticus; f, A. pratensis; g, A. albosangineus.*

WW. Annulus conspicuously double, with patches on the lower surface; sporophore readily staining yellow where bruised

Y. Sporophore stout, stem 1–3 cm. thick; annulus conspicuously radially-cracked on the lower surface, superior, ample, erect then pendant, double, white; *pileus* 8–12 cm. broad, convex, obtuse, smooth, white, flesh thick, compact, white, unchanging, odor and taste pleasant; *gills* subremote, rounded at the stem, ventricose, moderately broad, crowded, first white then grayish-pink, finally purple-brown; *stem* 8–11 cm. long, equal above the bulbous base, stuffed or hollow, smooth or somewhat floccose below, white; *spores* 7–10.5 × 4.5–5.5 μ ..... 23. *Agaricus arvensis* Schaeff.

YY. Sporophore thin, slender; stem 1.5 cm. thick or less; annulus with floccose patches below, but not conspicuously radially-cracked, superior, ample, thick, pendant, white; *pileus* 8 cm. broad, convex, satiny, smooth, white, flesh thick and white; *gills* rounded at both ends, ventricose, moderately broad, crowded, white, then pink, finally purplish-fuscous; *stem* 10 cm. long, equal, base usually with abrupt flat bulb, hollow, glabrous, white; *spores* 6–8 × 3–5 μ.
24. *Agaricus silvicola* Vitt.

DISCUSSION

1. **Agaricus diminutivus** Peck (FIG. 2), Ann. Rep. N. Y. State Mus. **26**: 59. 1874.
Syn.: *Psalliota diminutiva* Peck.

This species is not uncommon in the Puget Sound area, and is usually to be found in woods containing alder and maple. It is very well marked by its small size, thin, appressed rose-colored scales and very thin, persistent annulus. It is not likely to be confused with other small species of *Agaricus*. Sometimes the annulus clings to the margin of the pileus instead of the stem, or it may become appressed to the stem or be entirely torn away. The whole sporophore quickly stains saffron-yellow where handled, and invariably dries a deep orange-yellow. Kauffman (**10**, p. 245) also refers to these yellow stains, which apparently were not mentioned by Peck.

FIG. 2. *Agaricus diminutivus.*

2. **Agaricus micromegethus** Peck (FIG. 3), Ann. Rep. N. Y. State Mus. **54**: 152. 1901 (as *A. pusillus*); Ann. Rep. N. Y. State Mus. **94**: 36. 1905.
Syn.: *Psalliota micromegetha* Peck.

The stout, dwarfish stature, not unlike that of a miniature *A. arvensis*, readily distinguishes this species from other members of

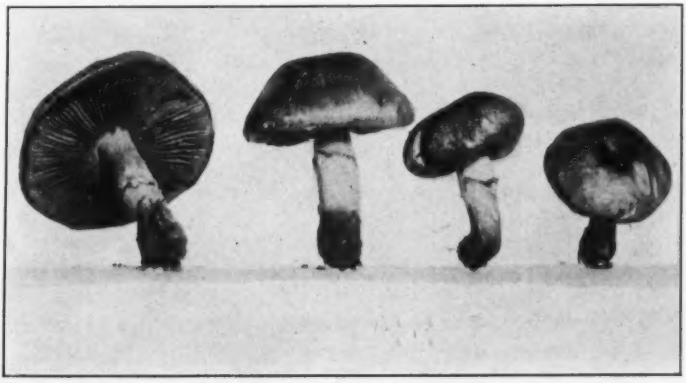

FIG. 3. *Agaricus micromegethus.*

the group of small forms. All parts of the sporophore turn deep saffron-yellow where touched; in fact, this discoloration may begin spontaneously soon after the plant is gathered, and may eventually obscure the original coloring of pileus, stem, and even the gills. In the pileus, however, only the cuticle is involved; the flesh does not change color where bruised. A strong odor of benzaldehyde is noticeable in the fresh plants. The specimens occurring in Washington differ from Peck's description cited by Kauffman (**10,** p. 243) in having somewhat larger spores and in not having the gills "gray at first." They were collected on the campus of the University of Washington, in grass in an open space.

3. **Agaricus dulcidulus** Schulz., in Kalchbr. Icon. Hym. Hung. tab. 17, Fig. 1; Fries Hym. Eur. 282. 1885.
Syn.: *Psalliota dulcidula* (Schulz.) Fries.

Zeller has reported this species from Oregon. It has not been found with certainty in Washington, but no doubt it occurs here. It differs from *A. diminutivus* in the absence of rosy-red scales and lack of a pink color during the development of the gills.

4. **Agaricus bivelatoides** Murr. Mycologia **4**: 297. 1912.
Syn.: *Psalliota bivelatoides* Murr.

5. **Agaricus comptuloides** Murr. Mycologia **4**: 297. 1912.
Syn.: *Psalliota comptuloides* Murr.

12. **Agaricus flavitingens** Murr. Mycologia **4**: 298. 1912.
Syn.: *Psalliota flavitingens* Murr.

19. **Agaricus subrufescentoides** Murr. Mycologia **4**: 299. 1912.
Syn.: *Psalliota subrufescentoides* Murr.

22. **Agaricus Hillii** Murr. Mycologia **4**: 298. 1912.
Syn.: *Psalliota Hillii* Murr.

All of these species were described by Murrill from material collected in 1911. The collections were made in the vicinity of Seattle, with the exception of *A. Hillii* which was reported from British Columbia (**15,** pp. 297–299). No subsequent collections of any of them have been made in Washington, nor did Murrill

deposit specimens of them in the herbaria of this region. Inquiry at the New York Botanical Garden has failed to locate any of these species.

For the sake of rendering a complete account of the genus, the above species are included in this article. Unless the type specimens can be located, however, a certain amount of doubt will always attend their determination. Murrill's original description of each species, quoted from Mycologia **4**, 1912, is included in the key.

6. **Agaricus albosanguineus** sp. nov. (FIG. 4; 1*g*).

Syn.: *Psalliota albosanguinea* sp. nov.

Pileo convexo, 8 cm. lato, albo vel brunneo-cinerescente in squamis, aequo, non striato, margine obtusato, superficie arida, molli, disco glabro, squamulis parvis, raris, appressis in margine; *carne* alba fracta illico sanguinea; *lamellis* liberis, ventricosis, remotioribus, postice rotundulis, attenuatis in margine, rubello-vinaceis tum purpureo-brunneis, fractis illico sanguineis; *stipite* 13 cm. longo, 1 cm. crasso, cylindrico, aequali vel basi leniter bulboso, solido, glabro, molli, albo, fracto illico sanguineo; *annulo* superiore, tenui, explicato tum refracto, simplici, membranaceo, albo; *sporis* 4–5 × 5.5–6.5 μ, ovatis vel ellipsoideis, levibus, uniguttulatis; in acie lamellarum cellulis sterilibus numerosis, racemosis, clavatis, simplicibus, usque ad 9 × 15 μ.

Hab.: ad terram in silvis, prope Seattle, Washington, Amer. bor.

Pileus convex, 8 cm. broad, white or with a faint tinge of grayish-brown on the scales, even, not striate, margin obtuse, surface dry, silky, glabrous at the center, with small, thin, appressed scales toward the margin; *flesh* white, quickly changing to blood-red where bruised; *gills* free, ventricose, somewhat remote, rounded behind, pointed at the margin, russet-vinaceous (R), becoming purple-brown, quickly becoming blood-red where bruised; *stem* 13 cm. long, 1 cm. thick, cylindrical, equal or slightly bulbous at the base, solid, glabrous, silky, white, quickly becoming blood-red where bruised; *annulus* superior, small, flaring then reflexed, simple, membranous, white; *spores* 4–5 × 5.5–6.5 μ, ovate to elliptic-ovate, smooth, uniguttulate; *sterile cells* (FIG. 1*g*) on the edge of the gills numerous, clustered, clavate, simple, up to 9 × 16 μ.

Habitat: on the ground under Douglas fir in the woods near Seattle, Washington.

The most striking characteristic of this species is the blood-red color immediately following a wound of the pileus, stem, or gills. This character is also found in *A. haemorrhoidarius, A. halophilus,*

and *A. exsertus* Viv. *A. albosanguineus* can be readily distinguished from the first two of the above-mentioned species by the absence of conspicuous brown scales on the pileus. The rather meager description of *A. exsertus* given by Saccardo (**19,** p. 998) agrees fairly well with the data on *A. albosanguineus.* In fact,

FIG. 4. *Agaricus albosanguineus.*

it might seem best to refer the latter to *A. exsertus,* were it not for the fact that there already exist two widely divergent interpretations of this species, given by Rea (**16,** p. 89) and Bresadola (**2,** p. 831), neither of which fits our form at all well. To add a third with a totally different concept would only increase the existing confusion.

7. **Agaricus haemorrhoidarius** Schulz., in Kalchbr. Icon. Hym. 29. 1872; Fries Hym. Eur. 281. 1885.
Syn.: *Psalliota haemorrhoidaria* (Schulz.) Fries.

In Europe the identity of this species has become involved with that of *Agaricus silvaticus* (see Note 11). The practice in America has been (by Kauffman, Peck, et al.) to maintain *A. haemorrhoidarius* as a separate species, and in the present article it seems best to do likewise. The writers have never collected any specimens which they felt could be referred with confidence to this species, and it is included in this paper solely on the report by Miss Jean Davidson of its occurrence in British Columbia (**3**).

8. **Agaricus halophilus** Peck (FIG. 5), Ann. Rep. N. Y. State Mus. **94**: 36. 1905.
Syn.: *Psalliota halophila* Peck.
Syn.: *Agaricus maritimus* Peck, 1899.

As decribed by Peck, *A. halophilus* differs from *A. haemorrhoidarius* chiefly in the very short, solid stem and the less scaly, differently-colored pileus. Hard (**7**, pp. 317–318) mentions and figures a form with broad umber scales. It is this form which has been found in Washington. Konrad and Maublanc (**12**, pl. 28) figure as *Agaricus silvaticus* subsp. *haemorrhoidarius* a fungus which agrees very well in stature, color and annulus with our specimens of *A. halophilus*, opening for consideration the question of whether or not the latter may be a mere form of *A. haemorrhoidarius*. In this connection, there is a possibility that the *A. haemorrhoidarius* reported by Jean Davidson from British Columbia may have been *A. halophilus* as interpreted in this article. The specimens figured in this article were collected on Whidby Island, in an open place, growing by a sidewalk.

9. **Agaricus subrutilescens** Kauff. Papers Mich. Acad. Sci. Arts and Letters **5**: 141. 1926.
Syn.: *Psalliota subrutilescens* Kauff.

Kauffman described this species from material collected near Mt. Hood, Oregon, in 1922 (**11**, p. 141). Since that time it has been found again in Oregon by Zeller, and also in Washington by the

FIG. 5. *Agaricus halophilus.*

FIG. 6. *Agaricus placomyces.*

writers. It is distinguished from similar scaly forms by its definitely vinaceous color. Neither *A. placomyces* nor *A. subrufescens* has this vinaceous tinge, and they differ also in spore size and character of the annulus. Another distinguishing character of *A. subrutilescens* is the conspicuous white floccose sheath of the stem. Although *A. subrufescens* and the members of the "*perrarus* group" also possess this character, it is not so pronounced as in *A. subrutilescens.*

10. **Agaricus placomyces** Peck (FIG. 6), Ann. Rep. N. Y. State Mus. **29**: 40. 1878.
Syn.: *Psalliota placomyces* Peck.

In the Puget Sound region, mushroom gatherers often refer to this species as the "woods mushroom" in which category they also include any silvan *Agaricus* with a scaly pileus, such as *A. subrufescens, A. perrarus,* etc. As a matter of fact, it is more usual to find *A. placomyces* growing in open deforested areas, especially those that are overgrown with bracken ferns. Less frequently, it may be found in an open pasture. It is common in Washington, being one of the few species of *Agaricus* that can be depended upon to appear every fall.

Apparently *A. placomyces* is a distinctly American plant. There is nothing just like it in Europe, save certain interpretations of *A. silvaticus* (see notes under 11). Its distinguishing characteristics are its size, the minute blackish-brown scales, the glabrous stem, and the conspicuously double annulus. The latter structure, when well developed, is precisely like the annulus of *A. arvensis,* and on this basis, together with a similarity in size and shape, Atkinson (**1**, p. 24) suggested that *A. placomyces* may be a woods-inhabiting variety of *arvensis.* The latter, however, has much larger spores.

Certain color changes of the flesh have been found to characterize the plant in this region. The base of the stem where buised quickly becomes bright yellow (cadmium yellow, R.), and this color then slowly changes to reddish-brown. The same colors appear more slowly and less intensely (baryta yellow, R.) in the upper stem and pileus, except that the yellow first becomes red and then brown. In the pileus it may finally change to purplish-red.

11. **Agaricus silvaticus** Schaeff. Icon. Bav. **4**: 62. 1774; Fries Hym. Eur. 280. 1885.
Syn.: *Psalliota silvatica* (Schaeff.) Fries.

Although the descriptions of *A. silvaticus* in European literature agree fairly well in the main, there is sufficient divergence among them to make it evident that no uniform concept of the species has yet been reached. The chief question seems to be whether or not *A. silvaticus* shall be made to include *A. haemorrhoidarius*. Ricken considers the two to be identical, Konrad and Maublanc include *A. haemorrhoidarius* as a sub-species under *A. silvaticus*, and Rea, Lange and Bresadola maintain that they are separate species. Various degrees of change in color of the flesh are assigned to *A. silvaticus*. Ricken and Lange describe it as quickly becoming red, Rea is noncommittal, Konrad and Maublanc describe it as slowly becoming reddish-brown, while Bresadola gives little if any change. Bresadola's figure of *A. silvaticus* (**2**; tab. 830) certainly resembles *A. placomyces* Peck, as found in the Puget Sound region. It is evident that his conception of *A. silvaticus* differs from that of many other European authors. Lange (**13**, p. 10), considering *A. silvaticus* an "equivocal" name, decides to abandon it altogether and describes his species as *A. sanguinarius* Karsten.

The above considerations should make it evident why it is so difficult to be sure that a specimen collected is or is not *A. silvaticus*. The writers feel disinclined to assign any of their collections to the species, and include it in this article chiefly on the basis of Murrill's report that he found it near Tacoma in 1911 (**15**, p. 295). Specimens from Friday Harbor labeled *A. silvaticus* are in the herbarium of the University of Washington, but lack sufficient field data to make their identity certain.

13. **Agaricus subrufescens** Peck (FIG. 7), Ann. Rep. N. Y. State Mus. **46**: 25. 1893.
Syn.: *Psalliota subrufescens* Peck.

This species of *Agaricus* is rather common around Seattle, its usual habitat being mixed stands of coniferous and broadleaf trees. The ample, flabby annulus with brown floccose patches on its under surface is distinctive, as are also the numerous small scales of the

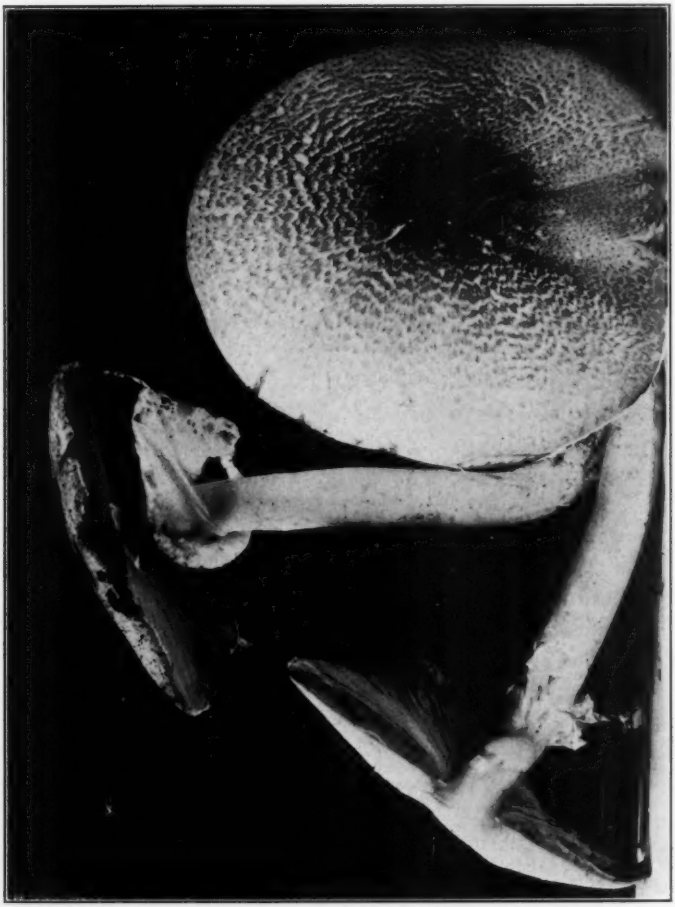

FIG. 7. *Agaricus subrufescens.*

pileus. These, it must be noted, are definitely reddish-brown in color, and thus differ from the scales of *A. placomyces*. Many American authors, notably Kauffman, consider *A. subrufescens* a valid species, but Atkinson (**1**, p. 23) intimates that it is probably the same as *A. silvaticus*. The latter, however, is generally considered to have a simple annulus and more or less of a color change of the flesh. More recently, Lange (**13**) has suggested that *A. subrufescens* is identical with *A. perrarus* and it seems to the writers, from observations of *A. subrufescens* as it occurs in western Washington, that there is much to recommend Lange's opinion. In size, scaly pileus, size and nature of annulus, the floccose-scaly stem, and the early pink stage of the gills, the two species are scarcely distinguishable. It is also worthy of note that both species have the edge of the gills densely beset with sterile cells. The main difference seems to be that the pileus of *A. subrufescens* lacks the straw-yellow color of *A. perrarus*, although it becomes yellowish when dried, and the cuticle turns yellow where bruised. Because the western *A. subrufescens* does not answer Kauffman's description (**10**, p. 239) in every particular (notably in spore size and color changes in the flesh), the writers consider it best to maintain it separate from *A. perrarus* until an opportunity arises to study typical *A. subrufescens* from the eastern states. For the time being, the Washington plants may be thought of as partaking of the characteristics of both species.

FIG. 7. *Agaricus subrufescens.*

14. **Agaricus villaticus** Brond. (FIG. 8; 1*c*) Pl. Crypt. Agen. 26, *pl. 7*. 1828; Fries Hym. Eur. 280. 1885.
Syn.: *Psalliota villatica* Brond.

Because of the rare occurrence in America of this species, additional notes are given regarding the form as it occurs in the Pacific Northwest, to supplement the brief description included in the key.

Pileus convex, becoming plane or remaining obtusely convex, margin exceeding the gills 1 or 2 mm., soon splitting into triangular patches, surface dry, smooth, center unbroken, covered everywhere else with small, distinct, appressed, silky squamules which are evenly distributed, color of the scales auburn (R), the flesh between them white or at length slightly ochraceous tinted,

FIG. 8. *Agaricus villaticus.*

where bruised staining baryta yellow (R), then becoming xanthine orange (R), often in large areas; flesh 1–2 cm. thick at the center, firm, white, quickly staining reddish-brown where bruised, especially toward the center, odor faint, not especially pleasant; *gills* free, approximate, broadly rounded toward the stem, pointed at the margin, narrow, 7 × 70 mm. or thereabouts, edges minutely white-fimbriate, extremely crowded, thin, of numerous lengths, color sorghum brown (R) or Hay's brown (R) or light seal brown (R) at maturity; *stem* generally tapering upward from the clavate-incrassated base, in some specimens nearly equal, firm, stuffed, surface densely floccose-squarrose below the annulus, the squarrae large and prominent, eventually almost or quite disappearing, above the annulus smooth and satiny, color ochraceous buff (R) below the annulus, above the annulus pallid or yellowish when young, becoming nearly ochraceous orange (R) in age; *annulus* ample, 2 cm. broad, pendant, not always free from the stem for its full width, double, very thick, the upper layer smooth, satiny, the lower layer felty-floccose, covering the entire lower surface with thick, close-set, felty patches which are ochraceous buff (R) in color; *sterile cells* on the edges of the gills inflated or cylindric, often consisting of a short row of cells (septate).

The descriptions by European authors of this species agree fairly well as regards macroscopic characters, but there are astonishing discrepancies in the matter of spore size. The spores of our plants are intermediate in size between the measurements given by Rea and those given by Lange. In all other particulars our specimens agree very well with the descriptions of Lange, Rea and especially Bresadola. (See notes 15, 16.)

15. **Agaricus augustus** Fries (FIG. 1*a*), Epicr. 212. 1836; Hym. Eur. 278. 1885.
Syn.: *Psalliota augusta* Fries.

16. **Agaricus perrarus** Schulz. (FIG. 9; 1*b*) Verhandl. Zool. Bot. Gesellsch. 493. 1879.
Syn.: *Psalliota perrara* (Schulz.) Fries.

Most European authors continue to regard these two species as distinct from one another, but Konrad and Maublanc (**12**, pl. 27) unite them under a single name, *Agaricus augustus*. It must be admitted that since they are very similar as regards size, ornamentation of pileus and stem, color, and annulus, they might easily

be confused even upon rather close examination. Nevertheless, Lange (**13**) has pointed out certain differences, one in the larger spore size of *A. augustus,* and another in the fact that the gills of *A. perrarus* soon become pink whereas those of *A. augustus* never

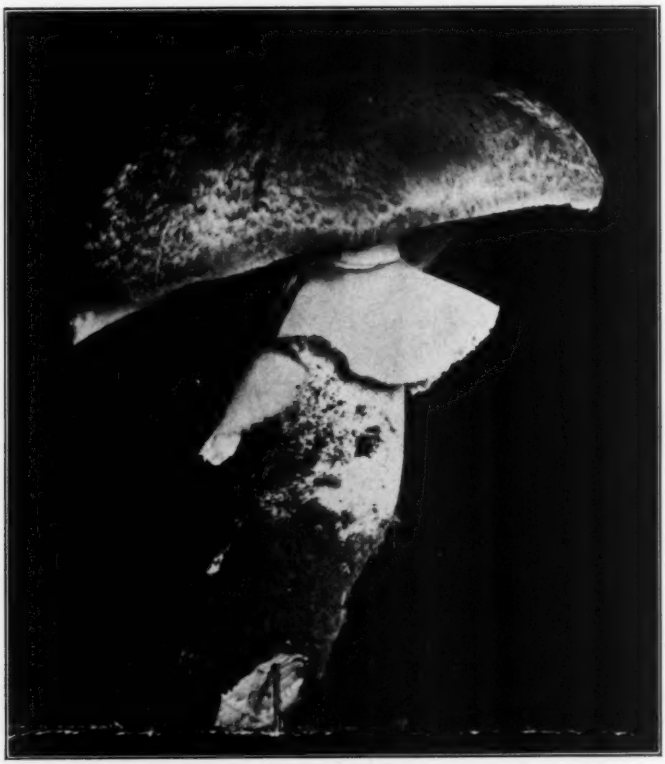

FIG. 9. *Agaricus perrarus.*

do so. These differences are borne out by observations of *A. perrarus* from Washington and of *A. augustus* from Oregon (**21**, p. 388).

The usual habitat of *A. perrarus* in this region is near the base of alder or maple trees, in rather open situations; less frequently it has been found associated with Douglas fir. It is a large plant,

measuring up to 35 cm. across the pileus, well distinguished by the yellow pileus with reddish-brown or brown scales, and the very voluminous annulus. Pileus and stem alike stain yellow to the touch, the bruised areas eventually becoming reddish-brown.

Because of the close resemblance between *A. perrarus* and *A. villaticus,* these two may be easily confused. The latter, however, has a short, stout stem which gives the whole sporophore a compact, squatty appearance. In addition to this, the annulus of *A. perrarus* is ample but rather flabby, whereas that of *A. villaticus* is thick and heavy, of the consistency of felt.

17. **Agaricus pratensis** Schaeff. (FIG. 1*f*) Icon. Bav. **4**: 42. 1774; Fries Hym. Eur. 279. 1885.
Syn.: *Psalliota pratensis* Schaeff.

This rather infrequently collected *Agaricus* is distinguished by its short, squatty habit, by its simple, often lacerate annulus, and by the predominantly grayish-brown color of the pileus, whose surface bears large, appressed scales, somewhat like those of certain *Lepiotae* in appearance. The above points, together with a total lack of color changes of the flesh, serve to separate *A. pratensis* from any of the numerous species of *Agaricus* with a scaly pileus, excepting the brown scaly form of *A. campestris.* The latter is quite similar in appearance, and probably can be best distinguished by the more intensely and persistently rose-colored gills, whose edge is devoid of sterile cells (see Note under 21).

One collection has been made (from Whidby Island) of *A. pratensis* in this region. The spore measurements agree well with those given by Ricken and Bresadola, but are larger than those of Rea. The edge of the gills is densely beset with rather short, clavate, hyaline sterile cells.

18. **Agaricus cervinifolius** Zeller, Mycologia **25**: 388. 1933.
Syn.: *Psalliota cervinifolia* Zeller.

This distinctive species rather recently described by Zeller (**21**, p. 388) from Oregon has not yet been found in Washington. Dr. Zeller has kindly permitted the writers to examine the type specimens. Even in the absence of the definitive fawn color of the young gills, this plant may be readily distinguished by its size, stature, narrow collar-like annulus, and scaly pileus.

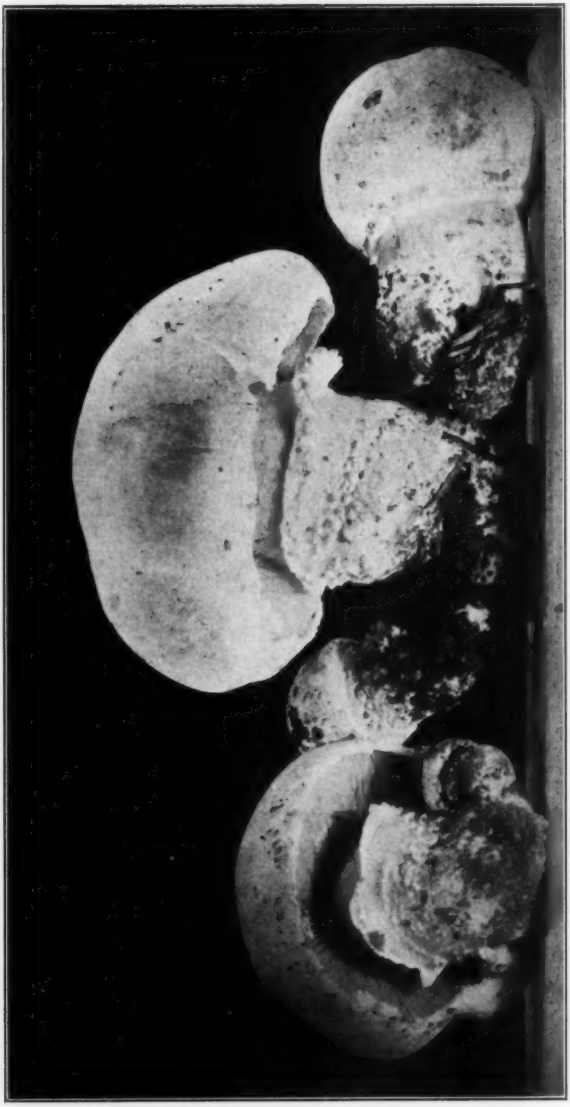

FIG. 10. *Agaricus Rodmani.*

20. **Agaricus Rodmani** Peck (FIG. 10), Ann. Rep. N. Y. State Mus. **36**: 45. 1884.
Syn.: *Psalliota Rodmani* Peck.

This species is not found frequently in western Washington. The only collections obtained were made on Whidby Island. It is more apt to be confused with *A. campestris* than with any other species, but it differs in having the center of the pileus ochraceous at maturity; in having a different type of annulus; in the lack of truly rose-colored gills, and in the smaller spores. The surface of *A. Rodmani* is like kid leather and will often bruise yellow, neither of which is true of *A. campestris.*

The double-edged annulus which is usually sufficient to characterize *A. Rodmani* is often not very well developed in the western plants. In case the double ring is not very evident, the plant may be recognized by its size and stoutness; by the kid-leather-like surface, and by the ochraceous center.

21. **Agaricus campestris** Fries, Syst. Myc. **1**: 231. 1821.
Syn.: *Psalliota campestris* Fries.

The common "field mushroom" is abundant here as in most other regions. The typical form, white and scale-less, is the one most commonly found, although occasional plants with appressed brown scales are found. Also, in the white form the cuticle may become more or less lacerate, even scaly at times, though the scales escape notice because they are not differentially colored. The stature, the thin, often evanescent annulus, white pileus, and bright pink gills afford certain identification of *A. campestris.* No part of the plant turns yellow, either upon bruising or in age or when dried.

23. **Agaricus arvensis** Schaeff. (FIG. 11; 1*c*) Icon. Bav. **4**: 72. 1774; Fries Hym. Eur. 278. 1885.
Syn.: *Psalliota arvensis* (Schaeff.) Fries.

24. **Agaricus silvicola** Vitt. (FIG. 12; 1*d*) Fung. Mang. 43. 1835; Fries Hym. Eur. 280. 1885.
Syn.: *Psalliota silvicola* (Vitt.) Fries.
Syn.: *Agaricus abruptus* Peck.
Syn.: *Agaricus abruptibulbus* Peck.

Of these two very similar species, *A. silvicola* is the more common in this region. Scarcely a season will pass in which it does not appear more or less abundantly in the coniferous woods. On the other hand, *A. arvensis* is comparatively rare. The collections made of it were from woods, not in the fields.

FIG. 11. *Agaricus arvensis.*

Modern European authors seem to have differences of opinion concerning the disposition of *A. silvicola.* Lange (**13**) considers it a variety of *A. arvensis,* while Konrad and Maublanc (**12**, pl. 29) maintain the two as separate species, an opinion also held by Rea. In America the situation was complicated by the introduc-

tion of Peck's *A. abruptibulbus,* a species which is considered synonymous with *A. silvicola* by Lange (**13**, p. 7), (**14**, p. 4). The writers feel no hesitancy in following Lange's disposition of the matter, as field observations have led them to consider the presence or absence of a flattened bulb much too variable a character to serve as a specific distinction. It is interesting to note

FIG. 12. *Agaricus silvicola.*

that Peck first described *A. abruptibulbus* as a variety of *A. arvensis.*

Whatever the relation between *A. arvensis* and *A. silvicola,* it seems generally conceded that the former is a large, thick-fleshed plant with a stout stem and an annulus whose lower surface is conspicuously radially cracked. The latter differs in being smaller, thinner, more slender-stemmed, and having the annulus only obscurely double.

Not only have specimens typical of each species been found in this region, but also intermediate forms are encountered. For in-

stance, plants with a notably slender stem and well-developed annulus of the *A. arvensis* type are sometimes collected. It seems evident that the two species are at least very closely related, perhaps as varieties, as suggested by Lange. This conclusion is further borne out by the fact that in collections of both species made in Washington, the spore size as well as the presence and character of sterile cells on the edge of the gills is practically the same.

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DISTRIBUTION, HOSTS AND INTERNAL TELIA OF PUCCINIA PARKERAE

C. R. STILLINGER [1]

(WITH 2 FIGURES)

During the last ten years *Puccinia Parkerae* Dietel & Holway has been under observation in the field. The following paper records a considerable extension in distribution, some new hosts, and the occurrence of internal telia for this rust.

DISTRIBUTION

Thus far the distribution of this rust has been reported from actual collections made only on the coastal region of Oregon and Washington. The original collection upon which the description of the rust was based was made at Seattle, Wash., June, 1894, by A. M. Parker. Jackson (**7**), in Oregon, reports collections near Mt. Jefferson and Hood River; in Washington, Hodson (**6**) reports collections at Seattle, Chequash Mts., and Winslow. As far as known the rust has not been definitely reported from British Columbia. Arthur (**1**) indicates that it also occurs in British Columbia, apparently in extension of the coastal region of Oregon and Washington. This appears to be an indigenous rust, yet it has been reported thus far only in this limited coastal territory, although its preferred host, *Ribes lacustre* (Pers.) Poir., has a wide distribution in both the eastern and western parts of the United States and in Canada (**4**).

The following collections indicate that the rust is of general occurrence east of the coastal region, over all of eastern Washington and northern Idaho. Likewise definite locations for the rust are reported for British Columbia. Except where credit is given to others, the collections were made by the writer.

[1] Associate pathologist, U. S. Department of Agriculture.

Ribes bracteosum Dougl.

C. N. Partington reported observing a single leaf infection on this host at Daisy Lake, B. C., in 1928. The specimen was lost, so the report could not be verified. This is the first report on this host.

Grossularia divaricata Dougl.

Daisy Lake, B. C., June 26, 1929, C. N. Partington, No. *2770*.[2] Found only on leaves. Infrequent. First report on this host.

Ribes sanguineum Pursh.

Scenic, Wash., July 31, 1920, No. *2868*. Occasional pustule on leaves only. Rare. First report on this host.

Ribes lacustre (Pers.) Poir.

Idaho: Priest Lake, Sept. 12 and 13, 1919, No. *1236;* Oxford Ranger Station, Clearwater National Forest, Aug. 20, 1921, No. *1497;* Musselshell Ranger Station, Clearwater National Forest, July 15, 1920, No. *907*, one bush with leaves, petioles, fruits, peduncles, and stems heavily infected, the infections in the woody stems giving the appearance of an aerial crown-gall attack (FIGS. 1, 2); Bovill, June, 1927, No. *2767*, and July 22, 1929, C. M. Chapman, No. *2768*, a general heavy leaf infection on approximately 2,000 plants; Warren, Aug. 24, 1920, G. A. Root, No. *1183*, a collection representing the southern known limit in this State, only a single infected leaf found; Bungalow Ranger Station, Clearwater National Forest, June 21, 1923, No. *1565*, two bushes with the infection so heavy on the leaves, petioles, fruit, peduncles, and stems that the bushes were being killed; Summit Lake, near Canadian boundary, in Kaniksu National Forest, July 23, 1923, P. S. Simcoe, No. *2356;* Monumental, Coeur d'Alene National Forest, July 27, 1927, No. *3011;* Clarks Fork, Aug. 15, 1928, E. L. Joy, No. *2998;* Marble Creek, July 8, 1929, No. *2769;* Kyle Creek, St. Joe National Forest, July 9, 1931, C. M. Chapman, No. *2997*.

Washington: American River, Yakima County, Sept. 8, 1922, L. N. Goodding, No. *56;* Eight Mile Ranger Station, Chelan

[2] Indicates numbers in writer's herbarium.

National Forest, Sept. 14, 1923, G. A. Root, No. *1956;* Metaline Falls, Aug. 9, 1924, No. *2202.*

Oregon: Government Camp, Mt. Hood, Aug. 14, 1920, No. *3012;* Parkdale, July 27, 1920, G. A. Root, No. *2241;* Swim, June 24, 1930, No. *2843.*

British Columbia: Mile 72, P. G. E. Ry., Aug. 13, 1927, C. N. Partington, no specimen in herbarium; Daisy Lake, Aug. 28, 1927, C. N. Partington, reported as abundant.

HOSTS

Although a careful watch has been kept for this rust on all the species of *Ribes* and *Grossularia* in Oregon, Washington, Idaho, and Montana, it has been observed chiefly on *Ribes lacustre.* However, it apparently will infect other Ribes, since one collection on *Grossularia divaricata,* one on *R. bracteosum,* and one on *R. sanguineum* have been made. These are the first collections reported on these hosts. Infections are reported as very sparse, indicating that the rust is chiefly restricted to *R. lacustre.*

Arthur (1) states that "this species is correlated with *Dicaeoma* (*Puccinia*) *Grossulariae* (Schum.) Kern, the telial characters of the two species being similar or identical, and the host of the short-cycled forms corresponding with the aecial hosts of the heteroecious form. This agreement doubtless indicates a common origin for the two species." If we are to assume that this is a possibility, it is indeed interesting to note the specialization which has developed, since *P. Parkerae* appears to be practically limited to one species of *Ribes* and only the telial stage has been found. On the other hand, *P. Grossulariae* (Schum.) Kern is very common all over this region on all species of Ribes and Grossularia, the aecia and pycnia occurring on the leaves while the uredinia and telia are found on Carex. In other words, we now have the telial stage for the two rusts on very different host plants widely separated botanically.

MORPHOLOGY

On the leaf the disease produces a reddish spot on the upper side similar to that produced by infections of the pycnia and aecia of *Puccinia Grossulariae.* Moreover, these reddish spots become

sunken into a cup-shaped cavity with very definite borders similar to that produced by a shot-hole fungus. Occasionally the spots do drop out. On the under side of the leaf opposite these reddish spots are found the dark brown telia (FIG. 1) varying from small specks to 6½ by 10 mm. They are generally located in the intervenal tissue with the ruptured epidermis evident around the edge of the round or oblong spot. The telia have a convex surface. They seldom coalesce even in very heavily infected leaves. Those on the main veins and midribs are usually much longer than wide, causing a distinct curved distortion of the vein. Occasionally a telium is found on the upper surface of a leaf directly opposite one on the under surface.

Also infection spots have been found which show very small telia arranged in a circular formation around the edge of the infected area somewhat in the manner of arrangement of the pycnia and aecia in *P. Grossulariae*.

Petiole infection is common on heavily infected bushes. These cause a definite hypertrophy of the petiole and a resultant bending. The infection may completely surround the petiole at one point or penetrate it, producing telia on both sides, thus weakening it so that it finally breaks at that point. Infections may occur as single spots or occasionally extend the full length of the petiole. In such cases it generally extends into the bud at the base of the petiole, not only killing the bud but extending down the pith into the center of the stem proper, spreading in both directions into the cortex and pith.

Frequently telia are found on the peduncles and fruit. The entire surface of the fruit may become covered with telia. These infected fruits shrivel and remain quite firmly attached to the raceme after the other fruit has fallen. Occasionally well-developed internal telia are found on the inner side of the pericarp, but none have been discovered in the seed. These internal telia are inverted and comprise a very broad, thin layer.

In two areas, Bungalow and Musselshell, Idaho, a very heavy stem infection was noted (FIG. 2). This is very unusual for this rust, consequently these collections are of considerable interest. The bushes where this type of infection occurred were growing in a very shady, moist site. They were heavily infected on the leaves,

petioles, fruits, and stems. Indeed, the bushes were so severely attacked that all the leaves were drooping on account of the additional weight of the numerous telia on the leaf, as well as the infection on the petiole. The fact that these bushes were so heavily

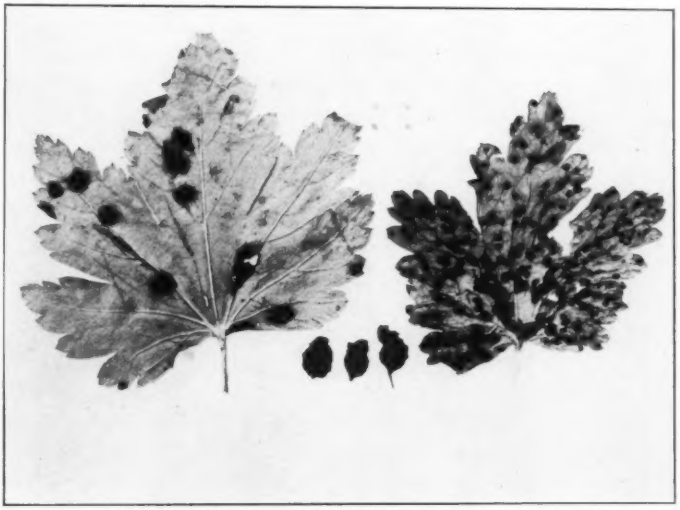

FIG. 1. *Puccinia Parkerae* D. & H. on leaves and fruit of *Ribes lacustre* (Pers.) Poir. Note the characteristic individual telia as well as the coalescing of the telia in some places. On the veins the telia spread considerably along the veins. The fruit surface is reduced to an almost solid mass of telia-producing surface.

infected is probably due to the great abundance of perennial telia which overwintered in the stem. Ordinarily, the infection, even on the leaves, is very light.

In some cases on the younger stems telia are similar to those on the leaf surface. On the older stems the infected area appears very much like aerial crown gall or similar to black knot, *Plowrightia morbosa* (Schw.) Sacc. These two conditions are well shown in figure 2. Sometimes quite large branches were so heavily cankered that they were killed.

Occasionally a distinct swelling of the stem was found, indicating the presence of the fungus, though the bark was still intact. An examination of these stems revealed the fungus.

FIG. 2. *Puccinia Parkerae* D. & H. on stems of *Ribes lacustre* (Pers.) Poir. Note the infection spreading from the leaf petioles into the stems as well as the cankered appearance on the older stems. The surface of all of the cankers is composed of a solid mat of telia.

Infection of the stem may take place directly upon the young annual growth or infection may extend from a petiole or young bud into the stem. All of these conditions are shown in figure 2. In some cases the infected spot is limited by callus growth, thus producing a small deep-seated canker. In other cases it extends in all directions into the stem.

Microscopical examination of these stem cankers revealed a continuous flat layer of telia on the surface. There was a heavy mycelial layer under these telia, sometimes parenchyma-like, but generally matted. The cortex under these spots was generally completely disorganized, the mass of fungus mycelium extending into the wood. The outer wood cells lying underneath this fruiting surface were of brownish content, and the medullary rays showed brownish strands of mycelium extending into the pith. The mycelium penetrated and broke down the pith cells so that often the pith consisted of a brownish disorganized mass of cells and mycelium.

In the immediate vicinity of the old cankers the cortex, wood, and pith were disintegrated and the cells enlarged. This enlargement of the cells as well as their segregation by the mycelium produced the enlarged condition of the stem.

Examination of wood an inch from the swollen portion or cankers of the stem revealed mycelium in the pith and occasional trachae filled with a yellowish substance. No mycelium was found in the wood cells. The general effect of the fungus resulted in a slight swelling of the pith, but the chief hypertrophy occurred in the bark. The wood ring was gradually swollen to an enlarged circle owing to the swelling of the medullary rays and increased in the size of the cells. It appeared that the mycelium extended lengthwise into the stem through the fibro-vascular bundle and laterally through the medullary rays into the pith.

At different depths in the cortex various stages of sori-like bodies were observed. Occasionally these were found partially embedded in the outer layer of wood. They gradually enlarged and became telia with a heavy mycelial mass at the base, the sides and tops having a thinner wall. Near the pith inverted telia were found. These internal telia were generally underneath surface-fruiting telia. Beneath these telia the infection was traced to the

center of the stem. In many cases the wood cells and medullary rays have partially broken down to the center of the stem, the whole forming a fan-like structure with the center of the stem as the base. Internal fruiting sori of rusts previously have been reported in seeds, fruits, petioles, leaves, and, in three cases, in stems. The internal telia in this case were quite in agreement with such structures as reported by Rice (**8**), Colley (**2, 3**), Dodge (**5**), and others. Since a good review of this subject with a complete bibliography is given by Rice (**8**), this information need not be repeated here.

SUMMARY

1. The distribution of *Puccinia Parkerae* is extended to eastern Washington, northern Idaho, and British Columbia.

2. The rust is primarily specialized on *Ribes lacustre*.

3. *Ribes bracteosum, R. sanguineum,* and *Grossularia divaricata* are reported as new hosts.

4. Stem and fruit infection of the host is reported for the first time.

5. Internal telia are reported in the fruit and stem of *Ribes lacustre*.

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NOTES AND BRIEF ARTICLES

Mr. H. W. Merkel, for many years Superintendent of the New York Zoological Park, and later of the Westchester County park system, died on February 28 in his home in Pleasantville. Mycologists will remember Mr. Merkel as the discoverer of the chestnut blight disease in the United States.—F. J. SEAVER.

CORRECTION

In a recent article in Mycologia **30**: 54–63, dealing with leaf-inhabiting fungi on sycamore the name *Cercospora platanifolia* Ellis & Ev. instead of *C. platanicola* Ellis & Ev. is employed. Attention is called to this unfortunate error so that further confusion may be avoided and the correct binomial may be employed. *Cercospora platanicola* is the conidial stage of *Mycosphaerella platanifolia* Cooke.—F. A. WOLF.

ON AND OFF ALASKAN TRAILS

Mycologists will find this volume recently issued by Dow V. Baxter and his collaborators interesting reading. While it is not in itself mycological, it might fittingly be referred to as "The Memoirs of a Meandering Mycologist," and consists of a diary on their various expeditions through Alaska. The information contained therein would be very helpful to anyone contemplating mycological exploration in that region.—F. J. SEAVER.

Mycological Foray

The Mycological Foray will be held at the Quebec Rangers School, Duchesnay, Quebec province, August 24–27 inclusive. Dr. Rene Pomerleau, forest pathologist of the Province of Quebec, will be in charge of local arrangements. There will be accommodations for mycologists and their families. He has arranged for the use of dormitory and dining facilities for $1.50 per day or

$0.50 per meal. All reservations for accommodations in the dormitories should be made through Mr. H. Roy, Director of the Quebec Rangers School, Duchesnay (Quebec). The school is located 20 miles northeast of Quebec City and can be easily reached by motorcar and railway. Additional information may be obtained by addressing Dr. Pomerleau. All mycologists, whether members of the Society or not, will be welcomed.

E. B. MAINS

NOTICE

The Managing-Editor wishes to call attention to the fact that the early volumes of MYCOLOGIA are still available at the exceptionally low price made, $50 for the first 24 volumes, plus the Twenty-Four Year Index volume. Individual volumes, or a smaller number of volumes, may be had at the same proportionate rate. Subscribers or members wishing to complete their sets should do so while this offer remains. For the most part, money derived from the sale of these early volumes is used in building up the Mycologia Restricted Endowment Fund. If one does not wish to buy for cash the exchange offer is also still open, fifty specimens of named fungi for each volume desired.—F. J. SEAVER.